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L.M.B.C. MEMOIRS.

XXV.

ASTERIAS

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Liverpool Marine Biology Committee.

L.M.B.C. MEMOIRS

ON TYPICAL BRITISH MARINE PLANTS & ANIMALS

EDITED BY W. A. HERDMAN, C.B.E., F.R.S.,
AND JAMES JOHNSTONE, D.Sc.

XXV.

ASTERIAS

BY

HERBERT C. CHADWICK, A.L.S.

(With 9 Plates)

THE UNIVERSITY PRESS OF LIVERPOOL LTD.
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April, 1923

EDITORS' PREFACE.

THE Liverpool Marine Biology Committee was constituted in 1885, with the object of investigating the Fauna and Flora of the Irish Sea.

The dredging, trawling, and other collecting expeditions organised by the Committee have been carried on intermittently since that time, and a considerable amount of material, both published and unpublished, has been accumulated. Thirty-six Annual Reports of the Committee and five volumes dealing with the "Fauna and Flora" have been issued. At an early stage of the investigations it became evident that a Biological Station or Laboratory on the seashore nearer the usual collecting grounds than Liverpool would be a material assistance in the work. Consequently the Committee, in 1887, established the Puffin Island Biological Station on the North Coast of Anglesey, and later on, in 1892, moved to the more commodious and accessible Station at Port Erin in the centre of the rich collecting grounds of the south end of the Isle of Man. A larger Biological Station and Fish Hatchery, on a more convenient site at Port Erin, has since been erected, and was opened for work in July, 1902. In 1920 the Committee ceased to exist and the management of the station was transferred to the Oceanography Department at the University of Liverpool. The name "L.M.B.C. Memoirs" is, however, still retained.

In these thirty-six years' experience of a Biological Station, where University students and amateurs form a large proportion of the workers, the want has been frequently felt of a series of detailed descriptions of the structure of certain common typical animals and plants, chosen as representatives of their groups, and dealt with by specialists. The same want has probably been felt in other similar institutions and in many University laboratories.

The objects of the Committee and of the workers at the Biological Station were at first chiefly faunistic and speciographic. The work must necessarily be so when opening up a new district. Some of the workers have published papers on morphological points, or on embryology and observations on life-histories and habits; but the majority of the papers in the volumes on the " Fauna and Flora of Liverpool Bay " have been, as was intended from the first, occupied with the names and characteristics and distribution of the many different kinds of marine plants and animals in our district. And this faunistic work will still go on. It is far from finished, and the Committee hope in the future to add still further to the records of the Fauna and Flora. But the papers in the present series, started in 1899, are quite distinct from these previous publications in name, in treatment, and in purpose. They are called " L.M.B.C. Memoirs," each treats of one type, and they are issued separately as they are ready, and will be obtainable Memoir by Memoir as they appear. It is hoped that such a series of special studies, written by those who are thoroughly familiar with the forms of which they treat, will be found of value by students of Biology in laboratories and in Marine Stations, and will be welcomed by many others working privately at Marine Natural History.

The forms selected are, as far as possible, common L.M.B.C. (Irish Sea) animals and plants of which no adequate account already exists in the text-books. Probably most of the specialists who have taken part in the L.M.B.C. work in the past will prepare accounts of one or more representatives of their groups. The following list shows those who have either performed or promised.

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Tubularia, R. C. Bamber.
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In addition to these, it is hoped that other Memoirs will be arranged for, on suitable types, such as Pontobdella, a Cestode, a Copepod and a Pycnogonid.

James Johnstone.

Oceanography Department,
University of Liverpool,
April, 1923.

L.M.B.C. MEMOIRS

No. XXV. ASTERIAS

BY

HERBERT C. CHADWICK, A.L.S.

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DISTRIBUTION AND HABITS.

Asterias rubens, Linn. (*Uraster rubens* of Forbes) (Pl. I, fig. 1; Pl. II, fig. 13) is probably the most familiar Echinoderm found in British seas. It is widely distributed around our coasts and occurs with more or less frequency on boulder-strewn beaches and stony bottoms from between tide-marks down to a depth of 100 fathoms. On the Eastern side of the North Atlantic it ranges from Finmark to Senegal, and it has been recorded from Japanese seas. In Port Erin Bay and the neighbourhood *Asterias rubens* does not occur in numbers between tide-marks, and the few specimens of average size found amongst the boulders at low water of spring tides have probably been thrown overboard by fishermen on their way from the fishing-grounds. In the deeper waters around the Isle of Man, however, the species is common and attains a large size. Specimens with rays approaching a foot in length are occasionally dredged. Almost every haul of the dredge or trawl includes a few specimens; and on the banks frequented by the line fishermen considerable loss is sustained on account of the frequency with which the bait, consisting principally of whelks, the abdomens of hermit crabs, and occasionally of limpets, is swallowed by starfishes of this and other species. *Asterias rubens* is a voracious animal, and its food appears to consist very largely of lamellibranch mollusca. Forbes (4) refers to some observations of M. Eudes Deslonchamps, published in the "Memoirs of the Linnean Society of Calvados," in which the author states that "when the tide was out, and while two or three inches of water remained on the sand, he saw balls of *Asterias rubens*, five or six in a ball, their rays interlacing, rolling about. In the centres of the balls were specimens of the mollusc *Mactra stultorum* in various stages of destruction, but always unable to close their valves and apparently dead." In much the same way *Asterias* has been seen to devour a sickly fish in the tanks of the Port Erin Aquarium. Should the fish be unable to raise itself from the bottom of the tank it is soon overpowered by the starfishes, which envelop it, their rays interlacing; and, if left undisturbed to the enjoyment of their meal, nothing remains at the end of a day or two but the skull and vertebral column.

Great as is the capacity of *Asterias* and its allies for swallowing large morsels of food entire, it is obviously unable to swallow a fish many times larger than itself, but in a case such as the one just cited it is able abundantly to satisfy its appetite by protruding its stomach through the mouth opening. Schiemenz (16) has shown that when a starfish wishes forcibly to open a bivalve mollusc, such as *Venus*, it seizes the shell with its numerous tube-feet and turns it round until the ventral margins of the valves are opposite its own mouth. At the same time, holding firmly to the substratum by means of the tube-feet of the distal portions of its rays, the starfish raises its disc and the proximal portions of its rays, the margins of which are pressed close together, into a regular mound, under which the mollusc is completely concealed. The tube-feet of the proximal portions of the rays are now brought into play, and by their united pull, which Schiemenz showed by experiment to be more than sufficient to overcome the resistance of the adductor muscles of the mollusc, the margins of the two valves are eventually separated widely enough to permit the intrusion of the stomach of the starfish, by which all the softer parts of the mollusc are quickly appropriated.

In some localities *Asterias rubens* appears to be gregarious. This is notably the case in parts of Morecambe Bay, at Hilbre Island in the Dee Estuary, in pools at Penmon in the Menai Straits, and underneath the pier at Bangor, where large numbers of individuals have been seen during the summer months in close association. Though capable of considerable activity, especially in quest of food, our species is a sluggish animal, and, at least in captivity, frequently remains in one position for hours. In a well-aerated aquarium tank, an attitude commonly assumed by the animal is with four of the rays clinging to the side of the tank and at the surface of the water, while the fifth ray is fully extended at right angles to the side and with the tube-feet in active movement.

When kept in aquarium tanks, even in circulating water, *Asterias rubens* occasionally and successively severs its rays from the disc, until, perhaps, only one is left. The detached rays and the disc may retain their vitality for even a day or two, but they invariably slough away and perish. The species, in common with its allies, has the power of repairing the effects of mechanical injury, and the effort to regenerate a severed ray is soon noticeable in a healthy specimen. It has been stated that a single ray can reproduce the entire animal, and Sedgwick (17) supposes that in this we have an "explanation of the so-called comet-forms, which consist of a large arm carrying a small disc with four small (sprouting) rays." The writer has never seen a comet-form in which the disc was proportionately smaller than its normally-sized single ray ; and to him it seems much more reasonable to suppose that the original rays had been bitten off by a predatory fish, or perhaps trapped by a threatened oyster or other mollusc. On physiological grounds the power of a detached ray to produce a disc may be seriously doubted.

CLASSIFICATION.

In his Report on the Asteroidea of the "Challenger" expedition Sladen (18) divides the class Asteroidea into two orders—the Phanerozonia and the Cryptozonia. The former order have well-developed marginal plates in two distinct rows ; the dermal branchiae are confined within the area bounded by the superior of these, and the adambulacral plates take a prominent place in the circum-oral ring of ossicles (Pl. III, fig. 26). In the Cryptozonia the marginal plates are reduced or obsolete and the dermal branchiae are not confined within a definite area. The adambulacral plates may or may not take a prominent place in the circum-oral ring of ossicles (fig. 25). The family Asteriidae, to which *Asterias rubens* belongs, is included in the Cryptozonia. It is characterised by the possession of a reticular abactinal skeleton, tube-feet apparently arranged in four rows and two kinds of pedicellariae.

METHODS.

Dissection of *Asterias* is best carried out upon specimens which have been hardened for a short time in 70 per cent. spirit. They may be killed in a sufficiently expanded condition by slowly adding strong spirit to the sea-water—just sufficient to cover them—in which they are living. To dissect a specimen make an incision with a scalpel in the body-wall at the base of one of the rays and just above the supero-marginal plates. With a pair of strong scissors carry the incision along the ray to its tip, keeping to the same level throughout. Carry the incision across the tip and along the opposite side of the ray to its base. When all the rays have been treated in this way (care being taken in cutting around the madreporite not to injure the subjacent axial sinus, stone canal and gastric haemal tufts), lift the extremity of one of the flaps of body-wall with a pair of forceps, and with a sharp scalpel cut through the mesenteries by which the hepatic caeca are suspended, working towards the base of the ray. To avoid injury to the stomach extreme care is necessary in cutting through the mesenteries by which it is suspended from the aboral body-wall of the disc. Before disposing of the body-wall note on its inner surface the apical longitudinal muscles and their intersection near the centre of the disc. Having studied the details of the digestive system, remove it by cutting through the retractor muscles of the cardiac portion of the stomach at their points of insertion and through the oesophagus as closely as possible to the mouth. Removal of the digestive system brings the principal features of the water-vascular system into view without further dissection. To see the axial organ *in situ*, take the largest specimen obtainable and make a longitudinal incision in the wall of the axial sinus as far away as possible from, but parallel with, the stone canal.

For the study of the histology of *Asterias* the writer has found corrosive-acetic mixture to be the best all-round fixative, but Bouin's Fluid also has given excellent results. Thorough decalcification of the tissues is necessary. For this purpose the writer has generally used a 5 per cent. solution of concentrated nitric acid in 70 per cent. spirit. The solution should be changed several times and its use continued for a day or two after the escape of bubbles of gas from the tissues has ceased. The pieces of tissue should then be thoroughly washed in repeated changes of 70 per cent. spirit, to which a little tincture of iodine has been added to remove all trace of the corrosive sublimate. For staining sections Heidenhain's iron haematoxylin, methyl-blue-eosin, Delafield's or Erlich's haematoxylin followed by eosin may be used.

EXTERNAL CHARACTERS.

The body of *Asterias rubens* (Pl. I, fig. 1 ; Pl. II, fig. 13) consists of a central disc and five rays which radiate therefrom. Specimens with six rays occasionally occur, and, more rarely, with four ; but in the latter case it is probable that one of the normal five has been lost as a result of injury. Both disc and rays are depressed from above downwards, but are gently rounded on the aboral surface. The rays are not sharply marked off from the disc and are rather stout, rounded, and taper very gradually towards the obtusely pointed or rounded tip. The rays are flexible and capable of extensive vertical and lateral movement. The aboral and lateral surfaces of both disc and rays bear numerous short, blunt or obtusely pointed spines. These are irregularly scattered, and often more numerous on the disc than on the rays. Traversing the median line of the aboral surface of each of the latter there is a single, slightly zigzag row of these spines, the prominence of which is enhanced during life by their purplish colour (Pl. I, fig. 1). In many specimens these rows of spines are connected together at their proximal ends by a pentagon of similar spines on the disc. Another well-marked row of spines along each side of the rays marks off their aboral from their lateral surfaces. Near the periphery of the disc, and opposite the angle between two of the rays, is a subpentagonal plate, the madreporite (Pl. I, figs. 1, 2, and 3), the convex surface of which is traversed by numerous close-set grooves which radiate from the centre to the periphery. A minute aperture, situated slightly excentrically on the aboral surface of the disc, is the anus (Pl. I, fig. 1, *an.*). If a living *Asterias* be examined with a lens, the aboral surface of the disc and rays and, to a rather slighter extent, the ventro-lateral surfaces of the latter, may be seen to bear large numbers of minute membranous projections, which together form a sort of velvety pile.

These are the papulae or dermal branchiae (Pl. II, fig. 15; Text-figure I, *dm. br.*; Pl. III, fig. 28). They are hollow, glove-finger-like organs, and communicate through the body-wall, in the irregular interspaces between the skeletal rods, with the perivisceral cavity. Minute pincer-like organs called pedicellariae are scattered more or less abundantly over the surface of the disc and rays. These are of two kinds, differing in size and structure, and will be described in detail below (Pl. I, figs. 4, etc.). The mouth (Pl. II, fig. 13, *mth.*) is situated in the centre of the under or actinal surface of the disc and is surrounded by a soft membranous peristome, in which no skeletal structures occur. A V-shaped ambulacral groove traverses the actinal surface of each ray. It is wide and deep at its proximal end and with the ray gradually narrows and becomes shallower as the tip is reached. The ambulacral grooves are fringed by two rows of rather stout and bluntly-pointed spines which bear clusters of major pedicellariae (Pl. I, fig. 4). In the interradial angles between the rays these spines project over and protect the peristome and mouth. A well-marked groove separates the outer of these two rows of spines from a third row of similar spines which, with another row, marks the infero-actino-lateral edge of the ray.

The ambulacral grooves lodge the tube-feet (Pl. II, fig. 13; Text-fig. I, *tb. ft.*). These are tubular, highly contractile and extensile locomotor organs, each of which, with the exception of the odd, terminal one, ends in a sucker-disc (Pl. II, figs. 16, 17 and 18). Just beneath the tip of each ray, and seated upon the base of the terminal tube-foot, or tentacle as it is frequently called, is a minute orange-coloured spot, the eye (Pl. II, fig. 13, *eye*). This consists of a cluster of deep invaginations of the ectoderm (Pl. VII, figs. 58, 60, 61 and 65, *opt. cp.*), lined by specialised cells, many of which develop the pigment which, in living specimens, makes the spot visible.

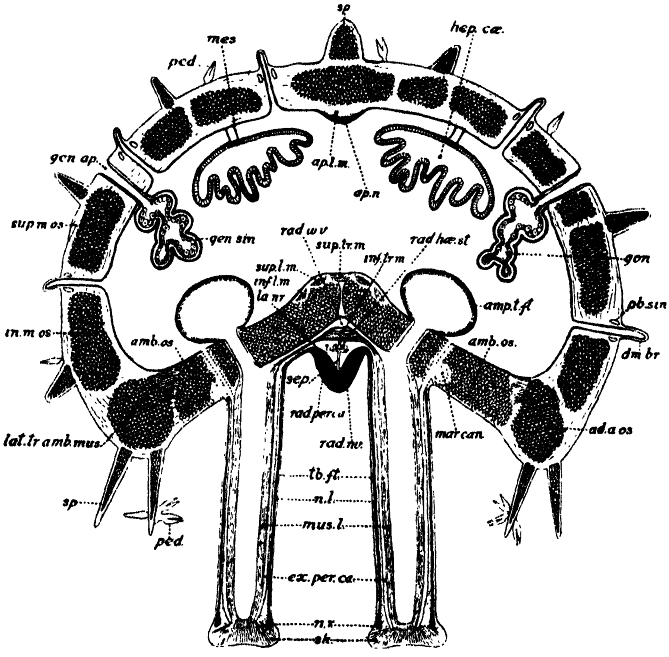

FIG. I. Transverse section of a ray near its proximal end. Diagrammatic.

The currents induced by the ectodermal cilia were investigated by Gemmill (7), who found that on the aboral aspect of the disc their direction was confused ; on that of the rays it was variable, but tended from the mid-radial line towards the lateral margin of the ray. In the interradial areas of the aboral aspect the direction was confused ; in those of the oral aspect it was centrifugal, i.e., away from the mouth; while in those of the lateral aspect it was aboralwards. The same direction was taken by the currents of the lateral aspect of the rays. On the madreporite the direction was from the periphery towards the centre of the plate. On the spines, pedicellariae and dermal branchiae the general direction was from base to summit, somewhat spirally on the former and latter. On the buccal membrane the current was wholly centrifugal, i.e., from the mouth opening to the margin. Along the bottom of the ambulacral grooves it tended from their extremities towards the mouth, while on their margins and between the bases of the fringing spines it was laterally outwards.

ENUMERATION OF RADII.

Modern writers on the Echinodermata are generally agreed that, on account of the morphological considerations which they believe to be involved, the enumeration of the radii of these animals should be based upon the position of the interradius in which the hydrocoel ring closes in the developing larva. The history of the development of a few species only is known; but it has already been shown that, in the different classes, the interradius in question presents considerable variation in relation to the position of the madreporite. Further, it must be noted that investigators of the development of more or less closely-allied species have arrived at opposite conclusions with regard to the question of orientation. Sedgwick (17) adopts and applies to all classes of the Echinodermata a method of enumeration based upon the assumption that the position of the stone canal and of the primary water pore is the same in all Echinoderms. His contention that this course conduces to clearness and precision in description is worthy of the fullest consideration, especially where, as in a text-book, all the classes of Echinoderms are described and compared. In the present work, however, the writer adopts the method of enumeration arrived at by MacBride (11), from a study of the development of *Asterina gibbosa*, and by Gemmill (5), from that of *Asterias rubens*. To orientate *Asterias* by this method the animal should be placed mouth downwards and with the interradius in which the madreporite is situated to the left of the observer (Pl. I, fig. 1; Pl. IV, fig. 31; Pl. V, fig. 43). The ray in front of this, the left anterior, is numbered I. Proceeding counter-clockwise, the left posterior ray is II, the posterior ray III, the right posterior IV and the right anterior V. Numbering in the same direction, the interradius in which the madreporite is situated is 1, and the anterior interradius 5. The latter is the interradius in which the hydrocoel ring closes in the developing larva and the one in which the anus of the adult is situated.

SKELETON.

The skeleton of *Asterias rubens* consists of a large number of variously shaped calcareous ossicles (Pl. III, figs. 24 to 30), lodged in the tough, leathery perisoma. These are composed of a spongy network of carbonate of lime, secreted by a meshwork of ill-defined cells of the dermis, which, in sections of decalcified portions of the disc and rays, are seen to fill the interspaces of the calcareous tissue. Unlike the component parts of the skeleton of the great majority of Echini, which take the form of flattened plates, joined together by their edges to form a rigid shell or test, the ossicles of the skeleton of *Asterias* are for the most part of rod-like form (Pl. III, figs. 28 and 30). The ambulacral skeleton, which supports the oral or actinal face of the animal, will be first described. The ambulacral grooves are supported by two rows of flattened rod-like ossicles, the ambulacral ossicles (Pl. III, figs. 24 and 27, *amb. os.*), which roof over the grooves. They are closely applied to each other by their flattened sides, and are articulated together in pairs at their inner ends (Text-fig. I, *amb. os.*). Both sides of every ambulacral ossicle are channelled by a half-pore, which corresponds in position with a similar half-pore in the next ossicle of the series, the two forming a complete pore through which a tube-foot communicates with its ampulla (fig. 27, *amb. pr.*). There is always one such pore between every two consecutive ossicles; and, owing to the perfect regularity with which the positions of the pores alternate, the whole series forms a sharply zigzagged line. The outer ends of the ambulacral ossicles abut upon the adambulacral ossicles, of which a series, corresponding in number with the ambulacral ossicles, borders the ambulacral groove on each side (Pl. III, fig. 24, *ad. a. os.*). They are small, half-moon shaped plates, flattened from side to side like the ambulacral ossicles, with which they alternate in position. With the exception of the first three or four, every second adambulacral ossicle throughout the series bears two stout, bluntly-pointed spines on its outer, rounded border, the alternating ossicles bearing only one. These are the adambulacral spines. They fringe the margins of the ambulacral grooves, over which, in virtue of their muscular attachment to their respective ossicles, they can be projected to cover and protect the tube-feet. In the adult starfish the first ambulacral and adambulacral ossicles, i.e., those nearest to the mouth (Pl. III, figs. 25 and 27, *amb. os.* and *ad. a. os.*), are much larger than the succeeding ones. Together they form the circum-oral or buccal ring. They are so closely bound together that in a living or spirit-preserved specimen the only indication of the line of junction is a rather large pore (figs. 25 and 27, *amb. p**). The two ossicles may, however, be dissociated by maceration for a few days in a 20 per cent. solution of caustic potash. When, as in the case of *Asterias*, the ambulacral ossicles are the more prominent components of the buccal ring (fig. 25), the latter is said to be "ambulacral." In *Astropecten* and its allies the adambulacral ossicles are much larger than the ambulacrals and form interradial projections, the buccal angles, and the buccal ring is called "adambulacral." There is some reason to believe that the first adambulacral ossicle in each series is the result of fusion of the original first and second ones (Pl. III, fig. 29). It is considerably larger than its immediate successors and bears two spines which project over the peristome towards the mouth. The next three or four ossicles are of gradually diminishing size and each bears one spine, but from this point outwards the alternation in number of spines described above obtains.

If a specimen of *Asterias* which has been well hardened in spirit be macerated for two or three days in a solution of caustic potash, and, after thorough washing in water, be dried, two regular rows of rod-like ossicles, which traverse the entire length of the ray, laterally, are brought into view. These are the "infero-marginal" and "supero-marginal" ossicles respectively (Pl. III, figs. 24 and 27, *in. m. os.* and *sp. m. os.*). Resting upon the first pair of adambulacral ossicles in each interradius is a broad and somewhat massive lozenge-shaped plate, to which the term "odontophone" has been applied, though it does not bear teeth (figs. 25, 26 and 27, *od.*). Its function appears to be that of a supporting buttress for the partly membranous, partly calcareous interbrachial septum which projects from the line of junction of two adjacent rays into the cavity of the disc. Belonging to the actinal skeleton, but situated on the abactinal surface at the tip of each ray is a collar-shaped ossicle which overarches the last formed ambulacral ossicles. This is the terminal plate. To bring it into view maceration of the tip of a ray of a fairly large specimen is recommended. As shown in fig. 78, Pl. IX, it is broad, flat, and of relatively large size in the very young starfish.

The ossicles which form the skeleton of the abactinal and supero-lateral surfaces of the disc and rays are longer or shorter rods, and are bound together by their overlapping ends to form an irregular network (Pl. III, figs. 28 and 30). The ossicles of the disc enclose interspaces of roughly triangular form, while those of the corresponding regions of the proximal portions of the rays are irregularly four-sided, their longer axes being at right-angles to the long axis of the ray. As the tip of the ray is approached the four-sided shape is gradually lost and the interspaces become irregular. Dermal branchiae arranged in the form of a circlet penetrate the soft perisoma which fills the interspaces (fig. 28, *dm. br.*). The calcareous substance of the spines is exactly like that of the skeletal ossicles. The spines are short, stout, and more or less bluntly-pointed. Besides the adambulacral ossicles the infero-marginal and supero-marginal ossicles bear spines which form well-marked rows, those borne by the former series being shorter and stouter than those borne by the adambulacrals. Those of the supero-marginal ossicles are shorter still and their tips more sharply pointed, features in which they closely resemble the spines of the abactinal surface.

PEDICELLARIAE.

As the pedicellariae are undoubtedly modified spines, and contain skeletal structures essential to the efficient performance of their function, they may be conveniently described here. The pedicellariae of *Asterias rubens* are of two kinds, called respectively "major" and "minor" or "straight" and "crossed" (Pl. I). A straight pedicellaria (figs. 4, 5 and 6) is of almost microscopic size and ovate form, its free end being bluntly pointed, while the attached end is broad and well-rounded. It contains three skeletal ossicles, two of which form opposing, pincer-like blades and are articulated with the third, or basal ossicle. The opposing faces of the blades are flat, their outer surfaces well-rounded and gradually tapering from base to tip. The whole organ is covered by the general ectoderm, which here contains large numbers of mucus cells (figs. 7 and 8, *muc. c.*). Movement of the blades is effected by three pairs of muscles, for the thorough study of which serial sections are necessary (figs. 7 and 8, *ax. mus.*, *oc. mus.* and *abd. f.*). The blades are opened by a pair of small muscles (fig. 8, *abd. f.*) which arise from the opposite ends of the basal ossicle and are inserted in the rounded outer faces of the blades. These are the abductor muscles. Two pairs of muscles arise deeply in the substance of the basal ossicle, the outer pair (*ax. mus.*) having a slightly deeper origin than the inner, and are inserted in the blades some little distance from their free ends, the outer pair extending further than the inner. The inner pair (*oc. mus.*) lie just below the ectoderm of the opposing faces of their respective blades, and, as shown in fig. 9, are broad and thicker at their lateral margins than in the middle. The outer pair are broadly oval in transverse section, and lie deeper in the substance of the blades. These two pairs of muscles are generally regarded as the adductors of the blades. The inner pair is probably the more powerful ; and their greater width and thickened margins will, doubtless, tend to prevent lateral movement at the moment of closure of the blades. All the fibres of which these muscles are composed are, roughly, as long as the muscle itself and of uniform diameter throughout. Each fibre has an elongate nucleus situated about the middle of its length. Straight pedicellariae may be sessile (figs. 6 and 7) or stalked (figs. 4 and 8). Both kinds occur in numbers on the abactinal and lateral surfaces of the disc and rays. The stalked form is borne in clusters by the spines forming the innermost row of those which fringe the ambulacral grooves (fig. 4). The stalk is flexible and capable of movement in every direction.

A crossed pedicellaria (figs. 10, 11 and 12) also contains three skeletal elements, a basal ossicle and two blades. The latter differ from those of the straight form in having their proximal ends produced to form handles which project beyond and partially cover the opposite sides of the basal ossicle, so that the whole organ resembles a small, bluntly-pointed pair of scissors. The distal ends of the blades are blunt and well-rounded. Movement of the blades upon the basal ossicle is effected by three pairs of muscles, the disposition of which differs considerably from that of the muscles of the straight pedicellaria. The blades are opened by a pair of small muscles which originate at the opposite ends of the basal ossicle and are inserted in the outer, rounded faces of the blades. They are closed by a pair of muscles which originate in the substance of the basal ossicle and, running transversely therefrom, are inserted in the handles of the blades on the opposite sides of the ossicle, and by an auxiliary pair which originate in the ossicle and take a straight course beneath the opposed faces of the blades, in the distal ends of which they are inserted. The flexible stalk of the crossed pedicellaria is traversed by a strand of elastic fibres, which divides beneath the basal ossicle to be inserted in the handles of the blades. The strands of a considerable number of pedicellariae become closely matted together to form, along with the muscle fibres, a prominent cushion around the larger spines (Pl. I, fig. 10). Muscular fibres originating in the spine are interwoven with the elastic fibres of the cushion, and, by their contraction, draw up the latter until the spine is more or less completely embedded in it. In virtue of their larger size in *Asterias glacialis* the crossed pedicellariae and the cushions on which they are seated may be studied to greater advantage in that species.

STRUCTURE OF THE BODY WALL.

The body wall (Pl. II, fig. 14) is composed of (1) a ciliated ectoderm (figs. 14, 15 and 16, *ect.*) which completely covers the whole of the body, including the spines and pedicellariae. It consists of a single layer of elongated columnar cells, covered externally by a thin structureless cuticle (*cut.*) and resting internally upon a basement membrane. Numerous mucus cells (Pl. I, figs. 7 and 8, *muc. c.*), sense cells and "mulberry" cells (Pl. II, fig. 19, *ml. c.*) are scattered amongst the ordinary ectoderm cells; (2) a cutis (Pl. II, fig. 14) which forms the greater part of the thickness of the body wall and consists of a gelatinous matrix containing nucleated connective tissue cells and fibres, muscle fibres and amoebocytes. The matrix is most evident in many places just below the ectoderm, where the connective tissue fibres traversing it are fine and sparsely scattered. In the deeper layers the connective tissue is much denser, and in this the calcareous ossicles which form the skeleton are deposited. As shown in fig. 14 the connective tissue forms an organic framework upon which the spongy calcareous substance is formed. Muscular fibres, forming an outer circular and an inner longitudinal layer, occur on the abactinal and lateral surfaces of the disc and rays, just beneath the epithelium which lines the body cavity. These fibres are fusiform and non-striated, and, owing to their affinity for eosin, are readily recognised in sections treated with that stain. The two layers are separated by a more or less well-defined layer of connective tissue and are not developed in the same proportions in every part of the body wall. The longitudinal layer is greatly thickened along the mid-abactinal line of the rays and forms a strong, projecting cord visible to the naked eye, the apical longitudinal muscle (Pl. II, fig. 14; Pl. VIII; Text-fig. I, *ap. l. m.*). The cords of all the rays unite at a central point in the disc. In addition to these two muscular layers there are developed in the actinal portion of the body wall a number of special muscles. These are (1) The superior and inferior transverse muscles of the ambulacral ossicles (Text-fig. I, *sup. tr. m.* and *inf. tr. m.*). These connect the inner ends of the ossicles, and their combined action tends to narrow and deepen the ambulacral groove. The superior muscle is the smaller and lies at the apex of the ambulacral ridge. The inferior muscle traverses the ambulacral groove between the radial water vessel (*rad. w. v.*) and the radial perihaemal canals (*rad. per. ca.*). (2) The superior and inferior longitudinal muscles of the ambulacral ossicles (Text-fig. I, *sup. l. m.* and *inf. l. m.*). These connect every pair of ambulacral ossicles with its fellows on either side. They traverse the narrow interspace between the flattened lateral faces of the ossicles and their combined action tends to shorten the length of the ray. (3) The lateral transverse ambulacral muscles (Text-fig. I, *lat. tr. amb. mus.*). These connect the outer ends of every pair of ambulacral ossicles with the corresponding adambulacral ossicles. Their action widens the ambulacral groove. (4) The longitudinal adambulacral muscles. These connect the flattened apposed faces of the adambulacral ossicles, and their action contributes largely to the lateral movements of the rays. In addition to the foregoing there are special muscles which effect the movements of the spines, especially the larger ones that fringe the ambulacral grooves. The muscles of the pedicellariae have already been described. The tube-feet are portions of the body wall specially modified for locomotion. Their histological structure corresponds closely with that of other portions of the body wall, and will be described in detail under the water-vascular and nervous systems. The dermal branchiae or papulae (Pl. II, fig. 15; Pl. III, fig. 28; Text-fig. I, *dm. br.*) are hollow processes of the body wall and, though extremely thin and devoid of calcareous deposits, exhibit the same histological structure. Their cavities are minute extensions of the body cavity, in which a constant streaming of the perivisceral fluid can be seen under a low power of the microscope. Around the base of each branchia and lodged in the connective tissue of the body wall is an annular space, the peribranchial sinus (fig. 15, *pb. sin.*), which is supposed to be derived from the body cavity. The dermal branchiae are highly sensitive to mechanical, thermal and chemical stimuli. A touch with a needle usually causes instant contraction. Deficiency of oxygen in the surrounding water causes prolonged contraction ; if the starfish be transferred to water containing oxygen in abundance the branchiae immediately respond by the fullest possible extension.

COELOM OR BODY-CAVITY.

The body-cavity is spacious and extends from the disc to the extremities of the rays. It contains the stomach, intestine, hepatic and pyloric caeca, gonads and the ampullae of the tube-feet, and is imperfectly partitioned, especially in the rays, by the mesenteries by which the stomach and hepatic caeca are suspended from the abactinal body-wall. It is lined throughout by a ciliated epithelium and contains an albuminous fluid in which there are many amoeboid corpuscles, variously called amoebocytes or leucocytes. It is highly probable that these cells are derived from the epithelium and that they discharge an excretory function. Durham (3) showed that when insoluble particles, such as those of Indian ink or carmine, are injected into the body-cavity they are ingested by the cells. Carried about by the currents induced by the cilia and, probably, to some extent by their own amoeboid activity, the cells make their way into the cavities of the dermal branchiae, wherein, should the excretory process be going on actively, small masses of the ingested pigment accumulate and become visible to the naked eye. Eventually the cells penetrate the delicate walls of the branchiae and, on reaching the exterior, disintegrate.

ALIMENTARY CANAL AND ITS APPENDAGES.

The actinal face of the disc is occupied by an uncalcified portion of the body-wall called the buccal membrane or peristome (Pl. V, fig. 43; Pl. VIII, *per.*). In its centre is the mouth, a small, rounded aperture when the animal is not feeding, but which is capable of great dilation by the action of radial muscular fibres which traverse the peristome. The mouth leads into a short oesophagus which rapidly widens into a spacious, thin-walled cavity, the cardiac portion of the stomach (Pl. IV, fig. 31; Pl. VIII, *stom.* (*card.*)). This organ practically fills the cavity of the disc, and slightly projects, radially, into that of the rays. Its wall is deeply and irregularly folded. It is eversible and retractile in virtue of the action of special muscles (Pl. V, fig. 43, *rt. m. st.*). Aborally it is separated by a sharp constriction from a much smaller sac, the pyloric portion of the stomach (Pl. IV, fig. 31; Pl. VIII, *stom.* (*pyl.*)). This, viewed aborally, is of pentagonal form (fig. 31), and is much depressed from above downwards. Its wall, like that of the cardiac sac, is much folded, the folds, especially those of the aboral wall, being for the most part radial. Into the five angles of the pyloric sac open the common ducts of five pairs of much sacculated diverticula, the so-called hepatic caeca (Pl. IV, fig. 31, *hep. cae.*). which are suspended by mesenteries from the inner face of the aboral body-wall, one pair in each ray (Text-fig. I, *hep. cae.*). Each pair originates from its common duct just beyond the confines of the cardiac portion of the stomach and traverses the ray almost to its extremity. Each diverticulum includes a median tubular cavity, into which open, alternately from right and left, a large number of irregular lateral channels. Into these, again, open the numerous sacculi into which the wall of the diverticulum is thrown (Text-fig. I, *hep. cae.*). The remaining portion of the alimentary canal is a very short tube which takes a nearly straight course from near the middle of the aboral face of the pyloric sac to the anus (Pl. VIII, *int.* and *an.*). The aperture through which the cavity of the pyloric sac communicates with that of the intestine is slit-like and is situated slightly excentrically in interradius 5/1. At a very short distance from this opening a much expanded and lobulated caecum, the rectal sac, opens into the intestine (Pl. IV, fig. 31 ; Pl. VIII, *re. sa.*). This varies considerably in size and as regards the number of its lobules. Beyond the opening of the rectal sac the rectum proper takes a straight course to the anus, which opens on the aboral face of the disc in interradius 5/1. The stomach is suspended from the aboral wall of the disc by a number of fine mesenterial strands, and the hepatic caeca are similarly suspended from the aboral walls of the rays by continuous mesenteries which gradually approach each other and eventually fuse near the tip of the ray (Text-fig. I, *mes.*). Their proximal ends are free, so that the space between them is part of the general body-cavity.

The stomach is furnished with five pairs of retractor muscles (Pl. V, fig. 43, *rt. m. st.*), which originate, one pair in each ray, along the sides of the axial ridge formed by the inner ends of the ambulacral ossicles and are inserted in the lateral walls of the organ. These muscles come into action when the cardiac sac is retracted after eversion for the prehension of food.

As stated above, the buccal membrane is simply an uncalcified portion of the integument. Its ectoderm cells (Pl. IV, fig. 32, *ect.*) are much longer than those of the general surface of the body, and their filiform ends are continuous with the delicate fibres of the underlying nerve layer (*n.l.*), which, at the periphery of the membrane, may be seen to be continuous with that of the circum-oral nerve-ring (Pl. VI, fig. 56, *per.* and *cir. or. n. r.*). Beneath this is the connective tissue layer (fig. 32, *c. t. l.*), the fibres of which form a spongy network. Next come two layers of muscular fibres, the inner (*in. m. l.*) concentric with the mouth, the outer (*ot. m. l.*) radial. Both layers, especially the outer, are thickest around the mouth and gradually thin out as the periphery of the membrane is approached. In almost immediate contact with the outer layer is the epithelium (*ep. per. cav.*) which lines the body-cavity.

At the oral aperture the ectoderm merges into the epithelial lining of the alimentary canal, in which numerous mucus cells appear (Pl. IV, figs. 33, etc.). The connective tissue layer is denser and its fibres more parallel. The fibres of the inner muscular layer are circular and rather more numerous, while those of the outer layer lie at an angle with the epithelium of the body-cavity. As the oesophageal wall merges into that of the stomach (Pl. IV, fig. 33) the cells of the epithelial lining (*ep.*) become longer and the mucus cells more numerous. The sub-epithelial nerve layer (*nl.*) appears uniformly in the cardiac portion of the stomach, and the filiform inner ends of many of the epithelial cells, bound together in bundles, pass through it to the basement membrane. Though in places but feebly developed the outer muscular layer is everywhere present. The inner one (*in. m. l.*) is not recognisable at all points.

The histology of the oral or lower face of the pyloric portion of the stomach (Pl. IV, fig. 35) is similar to that of the cardiac portion. Here the inner muscular layer is well-developed. At its periphery, however, an alteration in the relative development of the epithelial, connective and muscular elements takes place, and in the aboral or upper wall the epithelium accounts for nearly the whole of its thickness (fig. 36). In sections the nuclei of the epithelial cells appear as a broad and well-defined band, and the basement membrane is practically in contact with the epithelium of the perivisceral cavity, the connective and muscular elements being unrecognisable. In the intestine (fig. 37) the connective tissue layer is of great relative thickness, but the muscular fibres, if present, are not recognisable. The epithelial cells (*ep.*) are longest in the middle third of the length of the organ, and here a number of mucus cells are present.

In the rectal sac (Pl. IV, figs. 40 and 41) the epithelial lining is thrown into many strong folds, which project far into the lumen of the sac and are supported by ingrowths of the connective tissue layer. This is of a two-fold character, the tissue immediately underlying the epithelium being open and spongy, while a deeper layer consists of densely-matted fibres. The muscular layers, especially the inner one (*in. m. l.*) are well-developed. The fibres of the inner layer are cut transversely in sections of a lobule of the sac, while those of the outer layer are circular or oblique (fig. 41). There is, however, some difference at certain points in the relative development of the two layers, as well as in the direction of their fibres.

Excepting two points to be presently described, the thickness of the walls of the hepatic caeca (Pl. IV, figs. 38 and 39) is accounted for by the epithelium only, the basement membrane upon which the cells rest being scarcely separated from the epithelium of the perivisceral cavity. The epithelial cells are very long and have filiform inner ends. Amongst them are scattered many mucus cells of two kinds, the one large and rounded (fig. 38) and so closely crowded together as to give sections a vacuolated appearance under a low power ; the other of much smaller size, oval form and present in smaller numbers (fig. 39). At two points which are practically in the median line of each caecum the structure of the wall differs from that which forms the lateral sacculi. One of these is that portion of the wall of the caecum which lies between the points of attachment of the two mesenteries by which it is suspended from the aboral wall of the ray, the other is a deep fold which traverses its free oral face. In the latter the nuclei of the epithelial cells are much more densely crowded than are those of the sacculi (fig. 39), and in sections they appear as a fairly broad band. These cells bear specially long and powerful cilia. There is a well-marked nerve layer (*n. l.*) traversed by bundles of the filiform inner ends of the epithelial cells, and a muscular layer, the fibres of which are longitudinal or slightly oblique. In the short breadth of the wall which lies between the attachments of the mesenteries the muscular layer is absent. The other differences obtain but are not so well-marked.

WATER-VASCULAR SYSTEM.

This system consists of a circular vessel which surrounds the mouth, and five vessels which issue from it, at points corresponding with the five radii, and traverse the rays to their extremities, giving off numerous lateral branches which open into the cavities of the tube-feet (Text-fig. I, *rad. w. v.*). The circum-oral vessel (Pl. VIII, *cir. w. v.*) communicates with the exterior through the stone-canal (*st. ca.*), which runs aboralwards in interradius 1/2 and the pore canals of the madreporite (*mad.*). These vessels are lined throughout by a ciliated epithelium and contain an albuminous fluid in which amoeboid corpuscles occur.

As already stated, the madreporite is a sub-pentagonal plate of considerable thickness, situated near the margin of the disc in interradius 1/2 (Pl. I, figs. 1 and 2). Its diameter in adult specimens of *Asterias rubens* is about one-eighth that of the disc. Its convex external surface is traversed by numerous close-set grooves, which radiate, with slightly sinuous course, from the centre of the plate to its margin. Very few of these grooves, however, are continuous from centre to margin, and many do not extend more than a third of the distance. In a madreporite that has been isolated by maceration in a solution of caustic potash there may be seen, under a low magnifying power, at the bottom of the grooves, a considerable number of minute pores (Pl. I, fig. 2). These are the external openings of a corresponding number of minute canals, the pore canals, which traverse the thickness of the madreporite in a more or less vertical direction (Pl. VI, figs. 51 and 55, *p. can.*). The madreporite encloses a cavity of considerable relative size—the intramadreporite cavity (Pl. I, fig. 3, *int. mad. c.*) in the roof of which the line of insertion of the stone canal may be seen, besides the openings of a few of the collecting spaces into which the pore canals open. The cavity lodges also the dorsal sac and the ampulla of the stone canal (Pl. VIII). The pore canals gradually diminish in diameter as they traverse the substance of the madreporite (Pl. VI, fig. 55). They open into a number of collecting spaces, the great majority of which run towards the centre of the roof of the intramadreporic cavity and open into the funnel-like aboral end of the stone canal (fig. 51). A few of the more peripheral ones, however, are said to open directly into the axial sinus, an important cavity which may here be conveniently described. It is a flattened tubular space, lodged in the interbrachial septum 1/2, and is lined by ciliated epithelium (Pl. II, fig. 22; Pl. VI, figs. 55 to 57; Pl. VIII, *ax. sin.*). Its walls are tough and consist of longitudinally disposed muscular fibres and connective tissue. It extends from the abactinal to the actinal face of the starfish (Pl. VIII), and to its inner wall, that nearest to the vertical axis of the animal, the stone canal and the axial organ are attached by membranes (Plate VIII, *st. ca.* and *ax. or.*). The stone canal (Pl. III, fig. 27; Pl. V, fig. 43; Pl. VIII, *st. ca.*)

is a tube the walls of which are strengthened by ring-like deposits of calcareous skeletal matter, hence its name. Though lodged within the axial sinus it projects in adult specimens into the perivisceral cavity at the edge of the interbrachial septum. In passing oralwards from beneath the madreporite to its junction with the circum-oral vessel its course is more or less sinuous, especially at its oral end. The stone canal is not a simple tube. Throughout its length a ridge, the free edges of which form a pair of scroll-like lamellae (Pl. VI, figs. 55 and 57) projects into its lumen from the side opposite to that by which it is attached to the wall of the axial sinus. Its aboral end forms a funnel-like expansion which is incompletely attached to the madreporite in the roof of the intramadreporic cavity. Apertures in the funnel place the lumen of the canal in communication on the one hand with the axial sinus and on the other with the above-mentioned ampulla of the stone canal. This is a membranous diverticulum of the funnel (Pl. VIII, *amp. st. ca.*), the roof of which is in contact with the roof of the intramadreporic cavity, while its floor rests upon the dorsal sac. Its cavity communicates through the funnel with the pore canals of the madreporite and with the axial sinus. At its oral end the stone canal opens into the circum-oral water vessel (Pl. VIII, *cir. w. v.*). This is situated on the inner side of the buccal membrane, close to its peripheral margin (Pl. VI, fig. 56). Seated upon the inner wall of the circum-oral vessel and opening into its lumen there are nine small glandular structures, named after their discoverer Tiedemann's bodies (Pl. V, fig. 43). They are situated interradially in pairs, except in the madreporic interradius in which there is but one. In some families of Asteroidea, however (Astropectinidae), a pair of these bodies appears in the madreporic interradius. It is generally agreed that Tiedemann's bodies give origin to the amoeboid cells which occur in the water-vascular fluid. Other appendages of the circum-oral vessel are the Polian vesicles.

These do not occur in *Asterias rubens* ; but they are present and may be conveniently studied in species of *Asterina*, *Astropecten* and *Solaster*, and call for a brief description here. They are vesicular bodies of considerable relative size, and open by tubular ducts into the circum-oral vessel. They are situated interradially, and the number in each interradius varies in different species. In *Asterina gibbosa* there is one in each interradius except the madreporic one ; in that interradius of *Astropecten bispinosus* there are two, and one in each of the other interradii ; in *Solaster papposus* there is but one in all the interradii ; lastly there are species in which there are two, three or four in each interradius, and some in which several vesicles have a common duct.

The radial water vessels traverse the entire length of the rays and lie in the obtusely triangular space formed by the inner ends of the ambulacral ossicles and their transverse muscles (Text-fig. I, *rad. w. v.*). They give off on either side a number of branches, each of which opens into the tubular cavity of a tube-foot. The tube-feet are portions of the body-wall specially modified to subserve the function of locomotion. They appear to be arranged in the ambulacral grooves in four rows, but this is due to the fact that the lateral branches of the radial water vessels are alternately longer and shorter, an arrangement which obviously provides for a larger number of tube-feet in a given length of ray. There are thus two sharply zigzagged rows in each ambulacral groove. The cavity of each tube-foot communicates through one of the pores formed between the apposed faces of the ambulacral ossicles with its ampulla, a vesicular body which projects into the perivisceral cavity of the ray (Text-fig. I, *amp. t. ft.*). There is said to be a valvular arrangement at the junction of each of the lateral branches with the radial water vessel, the function of which is to prevent the passage backwards of the watery fluid contained in the tube-feet into the radial vessel when the former contract during locomotion. With one exception the free ends of the tube-feet are flattened and expanded to form adhesive suckers (Text-fig. I; Pl. V, fig. 46), the function of which will be seen later. The exception is the odd one at the extremity of each ray, the free end of which is obtusely pointed (Pl. VII, figs. 58 and 59). Its cavity forms the distal extremity of the radial water vessel.

The cells of the ectoderm which everywhere covers the external surface of the body show a change of character on the grooved surface of the madreporite (Pl. V, fig. 44). Here, on the sides and crests of the ridges which separate the grooves they are columnar and strongly ciliated. The fusiform nuclei stain very deeply with haematoxylin and in sections appear as a broad band occupying the deeper two-thirds of the cells. Pear-shaped mucus cells are freely scattered amongst the ciliated cells, especially on the crests of the ridges. Passing downwards for a short distance from the crests the length of the ciliated cells increases very slightly, thence it gradually diminishes until the bottom of the groove is reached. Passing into the pore canals the cells shorten rapidly and become cubical, somewhat irregular, and have rounded nuclei. Their cilia are weak and not always recognisable in sections. Cells of this character line the collecting channels of the madreporite and, extending into the axial sinus, remain practically unaltered throughout its length. At the aboral end of the stone canal, where, in part, its substance merges into that of the madreporite, the character of its epithelial lining contrasts markedly with that of the contiguous collecting channels. The cells suddenly become columnar and strongly ciliated (Pl. V, fig. 48), and very closely resemble those, already described, which cover the external surface of the madreporite. They are not, however, all of the same character. Sections, taken from near the aboral end of the canal, show that at the free edges of the two scroll-like lamellae which project into the lumen the cells shorten considerably, and their nuclei more nearly approach their outer ends. The whole of the external surfaces of the lamellae, i.e., those which face the opposite wall of the canal, are lined by cells of this character. The epithelial lining of the circum-oral water vessel, the radial vessels and their lateral branches to the tube-feet consist of small cubical cells with rounded nuclei.

Tiedemann's bodies (Pl. V, figs. 49 and 50) consist of a compact mass of branching tubules bound together by connective tissue and lined by cubical cells which contain pigmented concretions. The lumina of the tubules frequently contain rounded masses of cells which appear to have been budded off from the epithelium (fig. 50). There is evidence to show that these cells pass through the main duct of the gland (fig. 49) into the circum-oral water vessel, where they become the amoeboid cells of the water-vascular fluid. When present the Polian vesicles have a well-developed muscular layer in their walls, the lining of which consists of a connective tissue meshwork containing dividing cells. Cuénot states that these cells like those of Tiedemann's bodies, are discharged into the water-vascular fluid.

In the tube-feet the several layers of which the body-wall consists are found undisturbed by the formation of skeletal structures and are more clearly defined (Pl. II, figs. 16, 17 and 18). The ectoderm is covered, as elsewhere, by a delicate cuticle and is highly sensory, especially upon the terminal sucker discs, where sensory cells are very numerous. The sub-ectodermal nerve layer, which has already been seen in the structure of the body-wall is here well-developed and may be readily traced in sections from the sides of the radial nerve to the point where the tube-foot widens out to form the terminal sucker. Here the nerve layer thickens very considerably to form a well-defined nerve ring (fig. 16, *n. l.*). This will be described in greater detail as part of the nervous system. The muscular layer (*mus. l.*) is well-developed and, in a fully extended tube-foot, accounts for about one-third of its thickness, except at its proximal end, where the layer thickens considerably. Its fibres do not differ histologically from those of the body-wall and are wholly longitudinal. At the distal end of the tube-foot they converge towards the centre of the disc and end abruptly upon its proximal face. Proximally the muscular layer is continuous with that of the ampulla of the tube-foot, in which, however, the direction of the fibres is perpendicular to its wall (Pl. V, fig. 47). In transverse sections of the sucker (fig. 18) the fibres of which it is largely composed appear as wedge-shaped, radially disposed bundles, separated by connective tissue.

In spite of much experimental research the function of the madreporite is still imperfectly understood. Hartog (10) concluded from his experiments that the water-vascular system of Echinoderms is morphologically and ontogenetically a (left) nephridium. He found that the current induced by the cilia of the pore canals of the madreporite is outwards; and in opposition to the then generally accepted view that the madreporite is merely a filtering apparatus for sea-water entering the water-vascular system he urged that osmosis is sufficient to ensure the presence of water in the vessels and, consequently, the turgescence of the tube-feet during locomotion. While his contention as to the excretory character of the water-vascular system has not met with general acceptance his work has stimulated research. During recent years many experiments have been made upon the madreporite of *Asterias*, *Echinus* and other Echinoderms; and while the results are, perhaps, not conclusive, they lend some support to Hartog's statement that the direction of the current is outwards. Gemmill (5), however, points out that while "the pore canals themselves, together with their collecting stems, exhibit feeble ciliary action in an outward direction and thus continue the aboralward ciliation of the lining of the axial sinus," this "is not strong enough to compete with the inward suction of the stone canal and cannot accordingly prevent the entrance of water from outside into the stone canal, at any rate by the centrally-placed pores. . . . The following physiological results are thus rendered possible: (1) passage of water from outside through madreporite into stone canal; (2) prevention of entrance of foreign particles into stone canal; (3) passage of coelomic fluid from axial sinus into stone canal; (4) escape of axial sinus fluid through those marginal pore canals with which this sinus is most directly connected." The evidence that in the stone canal the direction of the current is oralwards (inwards) and that it has an important bearing upon the maintenance of pressure in the circum-oral and radial vessels appears to be well-nigh conclusive. In the stone canal of *Echinus esculentus*, which has no infolding of its wall and is, therefore, a simple tube, Gemmill found that the currents are always oralwards. Recently, however, Bamber (1) has shown that in the unexcised stone canal of this animal "there is a peripheral current towards the oral surface, apparently caused by cilia lining the canal, and a central current towards the madreporite." Hamann (8) suggests that the cilia of the low epithelium which, in the stone canal of *Asterias*, clothes the convex surfaces of the two scroll-like lamellae, may act aborally. In this connection the facts may be recalled that in certain species of *Asterias*, *Pentaceros* and *Gymnasteria* these lamellae are much wider than in *Asterias rubens* and become coiled, forming, in fact, two practically distinct canals within that enclosed by the outer wall; in some species of *Astropecten* a median septum divides the lumen of the canal into two distinct portions, into each of which a pair of scroll-like lamellae project, while in yet other species of *Astropecten*, *Luidia*, *Culcita* and *Ophidiaster* the entire lumen is traversed by irregular septa. To the present writer it seems highly probable that these complexities of structure indicate currents of different direction and intensity.

PERIHAEMAL SPACES.

Under the term perihaemal spaces are included the axial sinus, the circum-oral and radial perihaemal canals and the aboral circular sinus and its extensions. The first named has already been noticed. Aborally it extends to the madreporite, through the marginal pores of which it communicates with the exterior. It communicates also through the stone canal funnel with the canal itself and with the ampulla of the latter. At its oral end it opens into the inner circum-oral perihaemal canal (Pl. VI, fig. 56 ; Pl. VIII, *in. per. ca.* ; Text-fig. II). This is a ring-like space which surrounds the mouth, close to the peripheral margin of the peristome. It is separated by a slightly oblique septum from a similar but larger space, the outer circum-oral perihaemal canal (*out. per. ca.*). In each

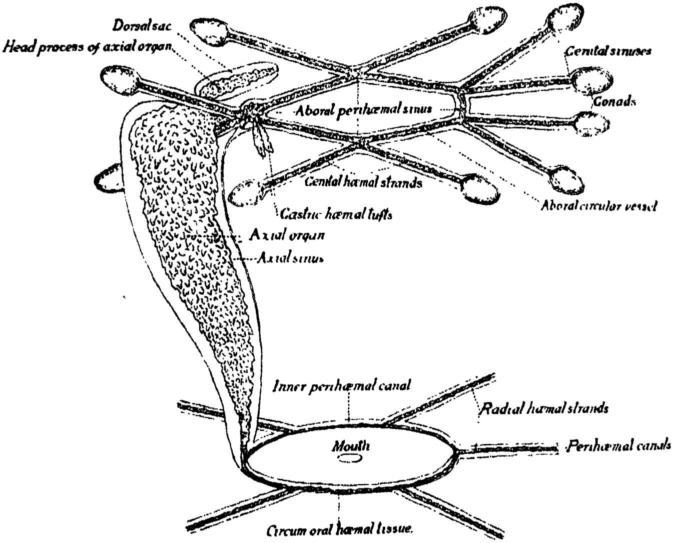

FIG. II. Schematic diagram to illustrate the axial organ and its relation to the oral and aboral circular hæmal strands and the strands of hæmal tissue proceeding therefrom, also the sinuses in which these structures are enclosed. Compare with Plate VIII.

mid-radial line the septum which divides the outer from the inner canal sends a vertical projection across its lumen. These vertical septa divide the canal into as many interradial portions as there are rays, each portion being prolonged into two adjacent rays. The prolongations traverse the rays to their extremities and form the radial perihaemal canals (Text-figs. I and II; Pl. VII, fig. 66, *per. hae. ca.*), two adjacent interradial portions of the circum-oral canal contributing to each radial perihaemal canal. The latter are divided longitudinally and throughout their length by prolongations of the above-mentioned radial vertical septa. The radial perihaemal canals are said to open laterally into sinuses in the walls of the tube-feet and, through these, with lateral canals which traverse the oral faces of the rays outside the ambulacra (Text-fig. I, *mar. can.*). Further, the lateral canals are said to communicate with the perivisceral cavity. The aboral perihaemal sinus (Pl. VIII, Text-fig. II, *ab. per sin.*) is a subpentagonal ring-like space which lies close to the inner (peritoneal) face of the aboral body-wall of the disc and sends prolongations, the genital sinuses, into each of the rays. It was formerly believed to be a complete ring and to be in open communication with the axial sinus; but Gemmill (6) has shown that in the madreporic interradius of *Solaster endeca* this sinus suffers an interruption, two blind ends being formed. Further, there is no communication with the axial sinus. In *Asterias rubens* practically the same conditions obtain, the aboral sinus being interrupted in the madreporic interradius and there being no open communication between it and the axial sinus.

HAEMAL SYSTEM.

The Haemal System, known also as the blood vascular or lacunar system, has been the subject of much research and controversy. Probably owing to its comparatively large size and to the fact that it may be exposed by dissection, the remarkable gland-like organ to which the names "heart," "ovoid gland," "dorsal organ," "central plexus" and "axial organ" have been successively applied appears to have been the first portion of the system to attract attention. Thus Kade in 1733 mentioned it, and in so doing was followed in 1809 by Spix. Five years later Konrad gave a short description of its external appearance and supposed it to be a gland. Shortly afterwards, in 1816, Tiedemann gave a more satisfactory account of its structure and appears to have been the first to call it a heart. He did not, however, draw a sharp distinction between the organ itself and the axial sinus in which it lies, and wrote indifferently of a "heart" and "heart-like canal." He was probably led to apply the former term to it by the discovery of its connection with the oral ring canal. The same term was subsequently applied to it by Siebold and Johannes Müller. Jourdain, followed by Greef, favoured the view of the glandular nature of the organ; and amongst later writers, including Hoffman, Teuscher, Ludwig, Perrier, Hamann and Cuénot, these two conflicting views as to the function of the organ are pretty evenly balanced. More recently the organ has been re-investigated by Durham (3), who adopted for it Carpenter's term "dorsal organ," and by Pietschmann (14), who reverts to the term "axial organ," adopted by the present writer. Lastly should be mentioned the work of MacBride (12), who dissents from the views of previous authors and applies the term "genital stolon" to the axial organ, believing that it is the place of origin of the genital cells. The axial organ lies in the cavity of the axial sinus, to the wall of which it is attached by a mesenteric fold (Pl. II, fig. 22, *ax. or.*). Along its entire length it is close to, and its aboral end partially envelops, the stone canal. Broad and comparatively massive at its aboral end (fig. 23) it gradually narrows and becomes a mere thread at its oral end, which rests upon the septum which divides the outer from the inner circum-oral perihaemal canal (Pl. VI, fig. 56

ax. or.; Text-fig. II). The colour of the living organ is pale brown, varying in different specimens to purplish. Its external surface is much lobulated. The epithelium which lines the axial sinus extends over it and is said to be ciliated; but the cells of the epithelium are hardly distinguishable from the underlying leucocytes, and if cilia exist they are not easily seen, nor does movement of particles in the surrounding fluid afford evidence of their presence. Examination of longitudinal sections under a moderately high power shows that the organ consists of tubular anastomosing strands, the walls of which are composed of an exceedingly thin membrane. The cavity of the axial sinus extends amongst these strands, forming intercanalicular spaces (fig. 56, *ax. sin.*). Intermingled with the strands are numerous fine fibrils, upon the nature of which authors disagree. When excised in the living state the organ shortens, and, for a time, contracts when touched with a needle. It is probable, therefore, that some of these fibrils are muscular. Pietschmann (14) among others describes and figures them as such. The whole organ is more or less densely crowded with cells of leucocytic nature (Pl. VI, figs. 52, 53 and 54), many of which exhibit pseudopodial processes and contain granules of the pigment which gives to the organ its general colour. In sections, large numbers of these cells may be seen within and upon the walls of the tubular strands. In all parts of the surface of the organ there may be seen also lobular swellings filled with a faintly staining coagulum. Here the leucocytes may be entirely absent or they may form a reticulum upon the surface of the swelling. An albuminous fluid, which stains faintly, completely fills the axial organ and is especially noticeable in the "head process." The latter is the aboral extremity of the axial organ (Pl. VI, fig. 55; Pl. VIII, *h. p. ax. or.*; Text-fig. II). It projects across a cavity—the dorsal sac (*dr. sa.*), larger than, and lying immediately below, the ampulla of the stone canal (*amp. st. ca.*) in the intramadreporic cavity. In histological structure the head process does not appear to differ essentially from the remainder of the axial organ. It consists of a delicate framework of connective and, probably, muscular tissue, enclosing an albuminous fluid in which, however, few leucocytes occur. This is especially the case in young specimens of a few millimetres to a few centimetres in greater diameter.

Near its aboral end, where it merges into the head process, and on the side nearest to the vertical axis of the starfish, the axial organ is continuous with a subpentagonal ring of tissue, closely resembling, if not identical with, that of the axial organ itself. This is the aboral haemal ring or aboral circular vessel (Pl. VIII, *ab. cir. v.*; Text-fig. II). It is lodged in the aboral sinus. At its five angles the ring gives off two strands which traverse the apposed walls of adjacent rays and, at their extremities, expand to form the genital organs or gonads. Here the sinus also expands and forms the genital sinuses (Pl. II, fig. 21, *gon.* and *gen. sin.*). Very close to its junction with the axial organ the aboral circular vessel gives off two tuft-like strands which penetrate the wall of the axial sinus and project into the perivisceral cavity. These are the "gastric strands" of Durham (3) and the "gastric haemal tufts" of Gemmill (5) (Pl. II, figs. 22 and 23; Pl. VIII, *g. hae. t.*: Text-fig. II). Their histological structure does not differ materially from that of the axial organ. The tubular anastomosing strands are, however, not so readily seen, but this may be due to the fact that the tufts are always densely crowded with leucocytes. In most series of sections the tufts are seen to be in actual contact with the wall of the cardiac portion of the stomach. Hamann (8) says that the channels in the tufts originate in the connective tissue spaces in the wall of the stomach, and in this he is confirmed by Gemmill (5). It has already been stated that the oral end of the axial organ rests upon the septum which divides the outer from the inner circum-oral perihaemal canal. Here it becomes continuous with another subpentagonal ring of haemal tissue, the oral blood ring or circum-oral blood vessel of authors (Pl. VI, fig. 56; Pl. VIII, *cir. or. hae. t.;* Text-fig. II). In serial sections this appears as lacunae of irregular size and shape which usually contain a few leucocytes suspended in coagulum. The circum-oral ring of haemal tissue supplies a radial branch to each of the rays. This, the radial blood vessel or radial haemal strand, traverses the vertical septum which, as we have already seen, separates the radial perihaemal canals (Text-fig. 1; Pl. VII, fig. 66, *rad. hae. st.*). The haemal strands are said to supply lateral branches to the tube-feet, and these are supported by transverse extensions of the septum (*sep.**).

The question of the real function of the various parts of the so-called haemal system cannot be said to be definitely solved. Pietschmann (14), who deals with the system at considerable length, asserts that on account of differences in histological detail the axial organ may be divided into three regions, each of which differs in corresponding function. To the gradually tapering oral extremity of the organ he ascribes an excretory function and thus to some extent supports the views of some of his predecessors. The middle portion he considers to be the seat of lymphocyte formation; while in view of the comparative richness in muscular fibres of the more massive aboral extremity including the head process of the organ, he suggests that it is contractile and may have a propulsive function. MacBride (12) takes an entirely different view of the nature and function of the axial organ and states that in it the genital cells originate, and that it should be termed the "genital stolon." The strand of tissue described above and called the aboral haemal ring he terms the "genital rachis" and suggests that it is merely the path along which the primitive germ cells migrate from the genital stolon to the genital organs which, as stated above, are merely enlargements of the extremities of the strands of tissue given off to the rays at the angles of the aboral haemal ring or rachis. Gemmill (5), the most recent writer on this system, discusses it under the term " Haemal," and includes in his survey the so-called gastric haemal tufts, which MacBride does not. He supports Ludwig's statement that these strands are haemal in character. He describes rhythmic contractions in the head process of *Asterias rubens* and other Asterids, the period of rhythm in the first-named being about 30 seconds. Experiments upon the axial organ itself yielded sometimes positive, sometimes negative results, the period of rhythm in the former cases being again about 30 seconds. Similar rhythmic contractions were observed in the gastric haemal tufts of specimens of *Asterias rubens* which were allowed to feed freely after they had been starved for some days, also slow contractions of the aboral haemal tissue. Taking these facts into consideration along with his own observations the present writer is inclined to support Gemmill's conclusions that in Asterids this system is really haemal and there is in it a circulation, the main purpose of which appears to be the transference of a nutritive fluid from the stomach to those systems of the animal which exhibit the greater physiological activity, viz., the nervous, reproductive and muscular systems. Attention may, however, be called to two closely-related points at which the evidence does not appear to be conclusive. Examination of a large number of serial sections of immature and sexually mature specimens shows that the gastric haemal tufts are not always in contact with the aboral wall of the cardiac portion of the stomach. It is possible that in such cases the two structures may have been torn asunder in course of dissection prior to fixation of the tissues. Again, assuming for the moment that during life the channels of the gastric haemal tufts are always in communication with the connective tissue spaces of the wall of the stomach, and that they are the channels of transference of the products of digestion from the stomach to the haemal system, it is remarkable that intercommunication should occur at only one small point in the whole circumference of the former.

NERVOUS SYSTEM.

The nervous system of *Asterias rubens* consists essentially of a plexus of fine fibrils and nerve cells which underlies the ectoderm and endoderm in practically all parts of the body. For purposes of description three parts may be distinguished, viz., the ambulacral or superficial oral, the deep oral and the apical; but it should be remembered that direct continuity between the first and the last named almost certainly exists. To that portion of the system which underlies the ectoderm, Sedgwick (17) applies the term ectoneural, and to that which underlies the epithelium of the alimentary canal the term endoneural.

If the tube-feet be cut away from one of the ambulacral grooves of a starfish which has been hardened in spirit, there may be seen traversing the entire length of the bottom of the groove a minute yellowish or brownish ridge. This is the radial nerve cord. At the distal extremity of the ray it forms a cushion-like thickening upon the base of the odd or azygos tentacle. Traced to the base of the ray the nerve cord may be seen to be continuous with a similar ridge which surrounds the mouth at the circumference of the peristome and forms the circum-oral nerve ring. Superficially, at least, the ambulacral or oral nervous system may be said to consist of the circum-oral nerve ring and the radial nerve cords. In transverse sections of a ray the latter appear as V-shaped thickenings of the ectoderm (Text-fig. I; Pl. VII, fig. 66, *rad. nr.*). The cord is thickest in the median line, i.e., where the two limbs of the V unite, and the latter gradually thin out towards their lateral margins, where they become continuous with the ordinary ectoderm of the ambulacral groove. The ectoderm cells of the nerve cords are columnar and of exceptional length (fig. 66) and their nuclei are situated near their outer ends. The nuclei contain the yellow or orange pigment which gives to the nerve cords their characteristic colour. The inner ends of the majority of the cells taper gradually until they reach the basement membrane and form a supporting framework for the plexus of nerve fibrils and ganglion cells which, as we have already seen, underlies the general ectoderm, but is here considerably thicker than elsewhere. Scattered amongst these so-called supporting cells are numerous sense cells, the filiform inner ends of which are continuous with the fibrils of the plexus. In longitudinal sections of a nerve cord many of the fibrils may be seen to run parallel with the axis of the ray : in transverse sections these appear as minute dots and give the section a very characteristic appearance. The circum-oral nerve ring is of exactly the same structure as the radial nerve cords. In vertical sections of the ring and neighbouring parts (Pl. VI, fig. 56) it may be seen to thicken rapidly from its inner margin, where it merges into the peristome, and to attain its greatest thickness much nearer to that margin than to its peripheral one. At the inner margin of the ring its specialised ectoderm cells pass gradually into those of the peristome, whilst the underlying plexus of nerve fibrils becomes relatively thicker and in sections of well-preserved material may be easily recognised. With greatly diminished thickness the plexus extends laterally from the radial nerve cords to the tube-feet, in the walls of which, at least on the side nearest to the nerve cord, it forms a distinct layer. Near the free end of each tube-foot, at the point where its tubular portion expands to form the terminal sucker, the nerve layer thickens greatly and forms a well-marked ring of nerve tissue (Text-fig. I ; Pl. II, figs. 16 and 17 ; Pl. VII, fig. 62, *n. l.*). Figure 62 shows that in ultimate structure this ring closely resembles the radial nerve cords. Many of the ectoderm cells overlying it are supporting cells, and their long, tapering inner ends reach the basement membrane. The nerve fibrils take, for the most part, a circular course. The sense cells of the ectoderm overlying the ring are so numerous as to form a distinct ring around the sides of the sucker. Thus it is highly probable that the suckers have a sensory as well as a locomotor function. We have already seen that at the base of the terminal or azygos tentacle the extremity of the radial nerve cord forms a cushion-like expansion. This is the optic cushion or " eye-spot " (Pl. VII, fig. 58, *op. cu.*). In this the histological details of the nerve cord are again reproduced ; and, in addition, the ectoderm is thrown into a number of pocket-like inversions (figs. 58, 60, 61 and 65, *opt. cp.*). In the living animal the eye-spot is rendered visible to the naked eye by a bright orange pigment lodged in the cells which line the pockets (fig. 65). The interpretation of the minute structure of this visual apparatus is one of the most difficult problems of the histology of the starfish, and the descriptions given by various authors differ materially. MacBride (12), following Pfeffer, says that each pocket is " lined partly by cells containing a bright orange pigment and partly by visual cells, each of which ends in a small clear rod projecting into the cavity of the pit." The present writer's results are more in accord with those of Cuénot (2). A figure by Pfeffer, which MacBride reproduces, shows the cuticle extending over the openings of the pockets. This is correct, and in some of the sections examined by the writer there appears to be a lenticular thickening of the cuticle over the openings, as shown in the figure. Cuénot, on the contrary, says " la cuticule qui revêt le cordon nerveux radial descend jusque dans les godets oculaires qu'elle revêt completement " ; and that " ne renferment aucune lentille ni conformation réfractante quelconque." The inner ends of the pigmented cells form a continuous lining of the pockets, and, at first sight, give the impression of a lining of colourless cubical cells (Pl. VII, figs. 61 and 65). The pigmented cells are, however, of great length and taper gradually to an extremely fine filament which plunges deeply into the subjacent nerve layer (fig. 64). The pigment is contained in the tapering portion of the cell, the granules being less numerous as the cell narrows and as the nucleus is approached. The latter is large and oval and is always situated at the point where the pigmented portion of the cell passes into the deep-seated filament. It projects from the side of the cell and is surrounded by a thin layer of cytoplasm. Projecting from the pigmented portion of the cell into the centre of the colourless portion which abuts upon the cavity of the pocket there is a minute rod with a rounded extremity. This is probably identical with the " visual rod " in Pfeffer's figure (MacBride (12), p. 446). The figure is somewhat indefinite, the boundaries of the colourless inner ends of the pigmented cells not being clearly shown. MacBride describes the " visual rods " as projecting into the cavity of the pocket; to the present writer they appear to be enclosed in the colourless portion of the cells (figs. 60 and 61). Lange and other authors have regarded the latter as a crystalline lens. Cuénot (2), on the contrary, contends that it is merely a cuticular structure and says that " dans des dilacérations, je les ai vus en continuité parfaite avec la cuticule des cellules non pigmentées environnantes."

Except in the absence of a terminal sucker the azygos tentacle does not differ essentially from the tube-feet (Pl. VII, figs. 58, *az. t.*, and 59). The cells of its ectoderm, especially those of its distal extremity, are almost wholly sensory. Mucous cells appear in numbers amongst them, especially at the tip and on the oral face of the tentacle (fig. 59). The nerve layer is well-developed, especially on the oral face, where, at a short distance from the tip, it forms a thickening similar to the nerve ring of an ordinary tube-foot. The connective tissue and muscular layers are relatively but feebly developed.

No specialised olfactory organ is known to exist in

Asterias rubens and its allies, but simple experiment shows that the sense of smell is by no means undeveloped. If kept for a few days without food a starfish will quickly detect a mussel removed from its shell or a bit of uncooked fish placed in its neighbourhood, and will crawl directly to it. In nearly every case, on reaching it, the morsel is enclosed between two of the rays, and the suckers of the tube-feet are applied to it, apparently with the object of testing its quality. It is then passed on to the mouth and, if not too large to pass through the oral ring of ossicles, is swallowed. By removing the eye-spots Romanes (15) showed that it is not necessarily through these organs that food is detected; and by progressively truncating the rays he found that the sense of smell is equally distributed throughout their length. By further experiment he found that it is almost certainly confined to the oral face of the animal. Experiments on *Asterias glacialis* led Prouho to conclude that the sense of smell is located in the tube-feet of the extremities of the rays. In certain of the Ophiuroidea, in which organs of special sense are unknown, the olfactory sense is developed to a remarkable degree.

That portion of the nervous system to which the term "endoneural" is applied above does not differ essentially from the ectoneural portion. It is developed in varying degree in all parts of the alimentary canal. It attains a considerable thickness and is easily recognised in the oral walls of both divisions of the stomach (Pl. IV, figs. 33 and 35) and in the specialised median folds of the hepatic caeca (fig. 39). In other parts of the latter (fig. 38) and in the wall of the rectal sac (fig. 41) it is scarcely recognisable.

The so-called deep oral nervous system consists of thickenings of the oral walls of the radial perihaemal canals which, like the radial cords of the ectoneural system, are united in the disc by a circum-oral thickening of the oral wall of the outer perihaemal canal. These structures are well known as

Lange's nerves (Text-fig. I; Pl. VI, fig. 56; Pl. VII, fig. 66, *la. nr.*). They are separated from the corresponding parts of the ectoneural system by a thin membrane only. Some, at least, of the cells of which these so-called nerve cords are composed, appear to be columnar and to have tapering inner ends; others, lying deeper in the cord, are rounded. It is very doubtful whether or not there is an underlying layer of fibrils. The function of these cords is said to be exclusively motor; and Cuénot figures twigs from their lateral edges to the muscles in the neighbourhood of the inner ends of the ambulacral ossicles. Should these twigs really exist they may be considered as supporting the morphological and physiological grounds upon which the nervous character of the cords has been assumed.

An apical nervous system has been described, consisting of single cords which lie upon the apical longitudinal muscles of the rays and, like them, traverse the entire length of the rays and unite in the centre of the disc (Text-fig. I; Pl. VIII, *ap. n.*). These cords are said to innervate the muscles of the aboral faces of the rays and to have a motor function. The writer has been unable to find any trace of this system in any of the large number of serial sections examined by him.

The physiology of the nervous system of *Asterias rubens* was investigated by Romanes (15), Jickeli, Preyer and others. The first-named found that a detached ray will crawl at the same speed and in as purposeful a manner as does the entire animal; and that, if inverted and laid upon its abactinal surface, it will immediately right itself. Section of the radial nerve at any point of a ray, whether detached or not, results in the destruction of physiological continuity between the tube-feet on either side of the point of severance. If the nerve cord of a detached ray be thus treated and the ray inverted, it experiences much greater difficulty in righting itself than does a detached but otherwise unmutilated ray. If the nerve be severed about the middle of its length, the two ends of the ray proximal and distal, behave somewhat differently. The proximal portion frequently arches itself, with its two ends resting upon the substratum. It may show signs of paralysis; and, if righted, owes the movement largely to the distal portion, which usually retains its power of movement for a considerable time, and is capable of using its tube-feet for the execution of righting movements. If all the radial nerves be severed at their proximal ends, or if the circum-oral nerve ring be severed between all the rays, the starfish loses all power of co-ordinating the movements of its rays. It moves slowly and aimlessly; and, if inverted, rights itself with difficulty and only after the lapse of some time.

MacBride (12) affirms that there is at least a physiological connection between the ambulacral and the deep oral nervous systems. He says (page 448): "Stimuli reaching the ectodermic ganglion cells are transmitted by them to the nervous part of the wall of the perihaemal canal (presumably Lange's nerve) and from that to the muscular portion of the same layer of cells."

REPRODUCTIVE SYSTEM.

The gonads (Pl. IX, fig. 67, *gon.*) are simply branched and much-lobulated sacs, lying free within the perivisceral cavity, except at their single point of attachment to the aboral body-wall, close to the proximal ends of the rays. The genital products of each gonad find their way to the exterior through a single efferent duct which traverses the body-wall and opens by a pore on the latero-aboral surface, close to the interradial line. The duct is lined by ciliated columnar epithelium. It expands slightly near its outer end, and at this point its lumen is partially interrupted by an uncalcified membrane having 4 to 7 perforations which lead directly to the surface. A pair of gonads is found in each ray. As the breeding season approaches they become much enlarged and extend centralwards almost into the body-cavity of the disc, and in the opposite direction nearly as far as the extremity of the rays. The strands of haemal tissue given off at the angles of the aboral blood ring extend to the roots of the corresponding gonads and terminate by dividing up into small branches which ramify upon their walls. The corresponding offshoots of the aboral sinus also extend to and completely enclose the gonads. The epithelium which lines the gonads and from which the spermatozoa and ova originate consists of cubical or polygonal cells. These also form the follicles in which the developing ova are enclosed. When fully developed the ovum measures 0·16 to 0·19 mm. in diameter. Yolk granules of a pale yellowish colour are uniformly distributed through the cytoplasm. The germinal vesicle contains a single large nucleolus and is slightly excentric. At first thin, the egg membrane becomes thicker during the later stages of growth and shows radial striations. During growth the ova are invested by follicle cells, which also fill in the interspaces between the ova.

The approach of the breeding season is indicated by lateral distension of the proximal ends of the rays ; but the sexes cannot be distinguished externally. While spawning *Asterias rubens* often assumes a characteristic position, with body bunched up and supported by the distal ends and in some cases the tips of the rays, which hold to the substratum by their tube-feet. In describing the phenomena of spawning, Gemmill (5) records a case in which, in about two hours, a starfish measuring 5½ inches in greater diameter was estimated to have extruded 2,500,000 eggs. In the neighbourhood of Port Erin spawning begins about the middle of February, when, and until the end of the month, considerable numbers of segmenting eggs, blastulae, gastrulae and early bipinnariae occur in the plankton of Port Erin Bay, and the early stages of development may be followed to advantage. Thereafter the number of developing larvae in the plankton diminishes very considerably, but the later bipinnaria stages occur sparingly until the middle of April. In the Firth of Clyde the spawning period occurs later than around the Isle of Man. Gemmill (5) obtained ripe ova at the beginning of April, and natural spawning was observed on April 23rd. The period of greatest activity, however, appears to be May and June.

DEVELOPMENT.*

In the process of fertilisation normally only one spermatozoon enters the egg. It first makes its way towards the centre of the egg and then towards the egg nucleus, with which it eventually unites. Immediately after, and at the point of entrance of the spermatozoon, the membrane of fertilisation appears and gradually envelops the egg. The spermatozoa are very active. and if many surround an egg their combined activity is sufficient to impart to it a rhythmic rocking motion. In segmentation of the egg the first two cleavages are vertical, the second being at right angles to the first. The next cleavage is horizontal, and results in an eight-celled stage in which the four upper cells are rather smaller than the four lower ones. This slight difference is maintained in the subsequent divisions, which are subregular. Even as early as the eight-celled stage there are occasional indications of the formation of a blastocoele cavity. The membrane of fertilisation persists until the developing blastula becomes ciliated and begins to rotate within it. The fully formed blastula is spherical, and about

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* In the account of the development of the larva of *Asterias rubens* here given it is not proposed to describe more than the writer has found it possible to follow by study of living larvae or of whole mounts thereof. The student who wishes to gain a more intimate knowledge of the subject especially of the development of the cœlomic cavities, is referred to the detailed account given by Gemmill (5) and the summary of the entire development by MacBride (13), both of which have been extensively laid under contribution in the present work.

0·2 mm. in diameter. Its wall consists of a single layer of cells which are ciliated externally. In this condition the blastula swims freely until about the middle of the second day after fertilisation, when the cells of the lower pole begin to lengthen, causing an appreciable thickening and slight flattening of the wall in this area. At the same time the larva lengthens in what may now be termed an antero-posterior direction and begins to rotate around its longer axis. Following upon the polar flattening just mentioned the wall of the blastula at this point forms a distinct ingrowth, which gradually extends as a narrow tube in the direction of the opposite pole and forms the archenteron. The external aperture of the archenteron is the blastopore. The larva is now a fully-formed gastrula (Text-fig. III, *arc.* and *bl.*). The blind end of the archenteron next expands slightly. Its cells proliferate, and many of them become amoeboid and stellate, and wander into the blastocoele to form the mesenchyme. On attaining its full length the archenteron bends slightly towards the future ventral surface of the larva, and at the same time the blastopore moves from its original position to the ventral surface. Meanwhile, a depression, lined by columnar epithelium, appears slightly in front of the middle

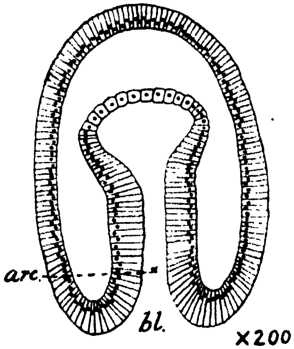

FIG III. Gastrula in optical section.

of the ventral surface. This indicates the future circum-oral field. The blind and gradually expanding end of the archenteron now extends backwards on each side, forming two hollow sacs (Text-figs. IV and V, *rc.* and *lc.*). These, ere long, are separated by constriction from the archenteron and become the right and left enterocoeles. Owing partly to migration and partly to lengthening of the larva the enterocoeles appear to travel backwards until, finally, they take up positions to right and left of the posterior end of the larval oesophagus (Pl. IX, figs. 68 and 69, *rc.* and *lc.*).

The archenteron becomes the alimentary canal of the larva. The stomodoeal pit deepens and the blind end of the archenteron with its developing enterocoele vesicles bends forward until the two meet and their cavities become continuous close in front of the place of separation of the vesicles (Text-fig. VII). Thus the larval mouth and oesophagus are formed. The latter is of considerable relative length. A well-marked constriction separates it from the capacious stomach which, at first pear-shaped, soon becomes globular (Pl. IX, figs. 68, 69, and 71, *stom.*). The posterior end of the stomach narrows rapidly and opens without definite constriction into the very short intestine and the longer rectum. Along the sides of the oesophagus a V-shaped band of strongly ciliated epithelium—the adoral ciliated band—makes its appearance (fig. 68, *ad. c. b.*). The angle of the V is posterior and in the mid-ventral line, and its two limbs are connected by a transverse, less strongly ciliated band which crosses the dorsal side of the oesophagus just behind the mouth. With the completion of the alimentary canal the larva begins to feed, and the cilia of the adoral band probably exert a powerful influence upon the convergence of food particles to the mouth. While the foregoing developmental changes are in progress the uniform ciliation of the larva seen in the blastula and gastrula stages undergoes modification. Even before the enterocoelic sacs separate from the archenteron, two broad but faintly defined bands of thickened ectoderm appear on the ventral face of the larva (Text-fig. V). One of these is anterior to the stomodoeal depression. Extending dorsalwards laterally it encloses the pre-oral field. The other band crosses the posterior end of the ventral face anterior to the anus. Extending at first slightly backwards the two ends turn forwards and pass obliquely along the sides of the larva to the anterior end of the dorsal surface (Text-figs. VI and VII). Here, on each side, the ends of the two loops unite, and for a short period, the ciliated band of the larva is unbroken, and represents a condition that is permanent in the auricularia larva of the Holothuroidea. Eventually, about the tenth or twelfth day, the connection between the two loops is severed at the point of junction and results in the formation of two distinct rings, named respectively the pre-oral and the post-oral. While these changes are in progress the band gradually narrows and becomes more clearly defined. Though reduced in numbers the cilia of the intervening areas remain long, and those of the circum-oral region serve an important food gathering function.

By the time when the enterocoeles have taken up their respective positions to the right and left of the stomach the left one is almost invariably larger than the right, and communication of its cavity with the exterior is early established by a tubular outgrowth which ascends to the dorsal surface of the larva and, meeting a slight inward dip of the ectoderm, opens thereon a little to the left of the middle line. The outgrowth becomes the pore canal of the larva and the aperture by which it opens to the exterior is the primary madreporic pore (Text-fig. VII, *p. can.* and *m. p.*). The wall of the pore canal is ciliated. In some cases, notably in larvae reared artificially, the right enterocoele sends up an exactly similar outgrowth which may or may not open to the exterior. The two enterocoeles now lengthen anteriorly until they meet and unite in the pre-oral lobe in front of the mouth. Posteriorly they

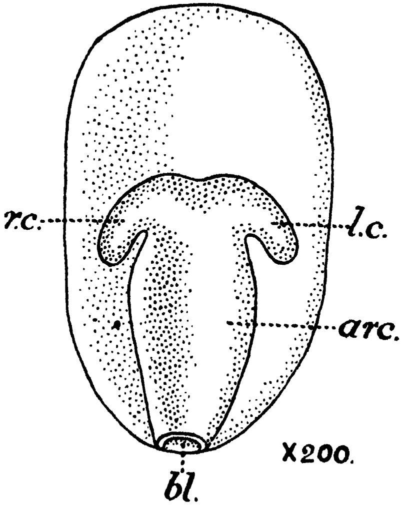

Fig. IV. Ventral view of larva, showing budding of coelomic vesicles.

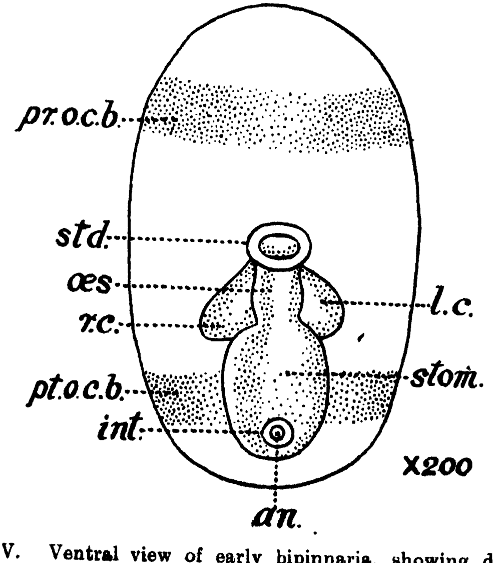

Fig. V. Ventral view of early bipinnaria, showing divisions of alimentary canal and ciliated band.

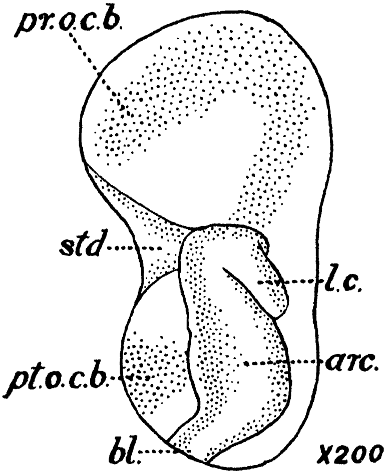

FIG. VI. Early bipinnaria viewed from the left side.

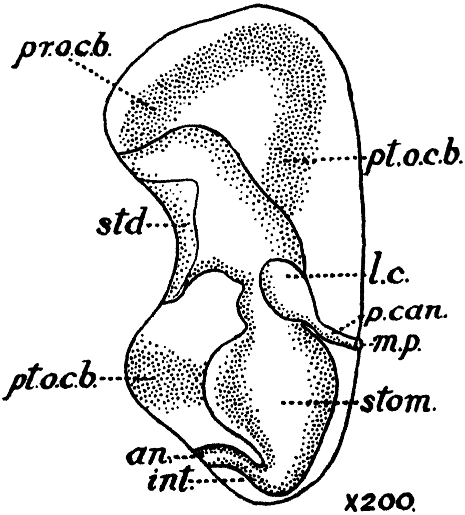

FIG. VII. Early bipinnaria viewed from the left side, showing completed alimentary canal and left coelom opening to exterior.

extend along the sides of the stomach and partially envelop it ventrally (Pl. IX, figs. 70 and 71). The left enterocoele, followed closely by the right, is now almost completely divided into anterior and posterior portions by a constriction which appears just behind the pore canal (fig. 70). The anterior portion thus becomes the left anterior coelom and the posterior portion the left posterior coelom (*l. a. coe.* and *l. p. coe.*). An outgrowth of the posterior end of the left anterior coelom, which soon assumes a five-lobed form, now appears. This is the rudiment of the water-vascular system of the adult starfish and is termed the hydrocoele (Pl. IX, figs. 72 to 74, I′-V′). Occasionally a similar rudiment is formed at the posterior end of the right anterior coelom. Shortly after the appearance of the hydrocoele a small, and at first almost solid, mass of cells makes its appearance in the blastocoele and takes up a position a little to the right of the mid-dorsal line. This is the madreporic vesicle or dorsal sac. Eventually it enlarges and becomes thin-walled. When the development of the larva is fairly well advanced (about the 35th day) it begins to pulsate. Gemmill (5) found the pulsations to continue from that time until further observation became impossible owing to increasing opacity of the larva.

Three regions may now be distinguished in the coelom, to which the terms anterior, middle and posterior are applied (Pl. IX, fig. 70, *l. a. coe.*, *l. m. coe.* and *l. p. coe.*), but it should be remembered that these terms do not necessarily indicate separate morphological units.

As a result of growth more rapid than that of the adjacent body-wall the ciliated band becomes more and more sinuous and eventually forms a number of lobe-like outgrowths (Pl. IX, figs. 71 to 73), one of which is anterior and unpaired, while the remainder are paired and disposed at intervals along the sides of the larva, thus giving it a " bipinnate " appearance, whence the term bipinnaria now applied to it. The anterior unpaired process (*m. d. p.*) is termed the median dorsal; proceeding from the anterior to the posterior end of the larva the paired processes are respectively the antero-dorsal (*a. d. p.*), the postero-dorsal (*p. d. p.*), the postero-lateral (*p. l. p.*) and the post-oral (*p. o. p.* or *pt. or. p.* in fig. 73). All the paired processes, especially the last-named, have considerable power of movement.

The formation of the madreporic vesicle, the assumption of a five-rayed form by the hydrocoele and the outgrowth of the ciliated processes bring the larva to its full development as a free-swimming organism. The further developmental changes, now to be indicated, bring with them change of habit and prepare it for adult life. In other words, metamorphosis takes place.

From the anterior end of the larva, and between the pre-oral and post-oral ciliated bands, there grow out three rather short but stout arms with slightly expanded and papillate ends, and containing diverticula of the anterior coelom. One is median and dorsal, the other two lateral and slightly posterior to the median one. These are the brachia (Pl. IX, figs. 72 to 74, *m. bra.*, *r. l. bra.* and *l. l. bra.*), and with their development the larva becomes a brachiolaria. The free ends of the brachia apparently act as suckers, and by means of them the larva occasionally attaches itself. As the brachia grow out they carry with them loops of the pre-oral ciliated band. At the base of the median brachium and between the two lateral ones a disc of glandular ectoderm with a thickened edge appears. This is the organ by which the brachiolaria permanently fixes itself to the substratum (Pl. IX, figs. 72 to 74, and 76, *su.*). By this time the larva has become differentiated into two well-marked regions: an anterior one to which the term stalk is now applied, and a posterior one known as the disc. The former consists of the pre-oral lobe of the larva, and contains its mouth, oesophagus and anterior coelom; the latter is virtually the disc of the future starfish. It contains the larval stomach, intestine, hydrocoele and right and left posterior coelom (figs. 73 and 74). After permanent fixation of the brachiolaria the stalk gradually shortens. The outgrowth of the rays of the future starfish is now indicated by the appearance of five lobes around the margin of the disc. As a result of the growth and extension of the left posterior coelom, the right posterior coelom and the disc become displaced and eventually take up a position at the posterior end of the larva. The stone canal, an open groove of ciliated epithelium, beginning just beneath the inner end of the pore-canal, now becomes a tube by the incurving and meeting of its edges. The five lobes of the hydrocoele are the rudiments of the radial water vessels of the adult. They extend radially, each one corresponding with one of the lobes of the disc ; and before metamorphosis of the larva is complete they develop two pairs of lateral lobes which are the rudiments of the primary tube-feet. The blind end of the original lobe forms the azygos tentacle of the adult. The stomach of the adult first appears as an outgrowth from the left side of the larval stomach. At the same time the rudiments of the pyloric caeca of the adult appear as pouches which grow out from the larval stomach and extend into the developing arms. The larval stomach becomes the pyloric portion of the stomach of the adult. The adult mouth is formed by fusion of the adult stomach with the ectoderm. The rectum does not appear until late and is formed from the proximal end of the larval intestine. At a still later period the anus of the adult appears in the aboral right interradius. By the time when the young starfish is ready to lead a free life the ciliated band of the larva has practically disappeared and the first-formed tube-feet have become functional. The stalk of the sucker, resulting from the reduction of the anterior portion of the larva, gradually lengthens until it becomes attenuated and finally breaks at a point near its proximal end and sets the starfish free (Pl. IX, fig. 76).

The rudiments of the calcareous plates which form the skeleton of the adult starfish make their appearance as minute spicules which, by lateral growth only, soon become thin, reticulate plates (Pl. IX, figs. 75 and 78). The first plates to appear are the five terminals (*tml.*) so called because they maintain their positions at the tips of the rays throughout life. The next plates to appear, also five in number, have been variously termed basals, genitals or inter-radials by authors. These are situated in the inter-radii (*int. rad.*) and form a circlet within that of the terminals. One of them gradually surrounds the madreporic pore and eventually becomes the madreporite of the adult. Next appears a single plate, the dorso-central (*dor. cen.*). This does not at first lie in the centre of the disc, but a little to one side of that point in the direction of inter-radius II/III. On the oral face of the rays, which by this time are extending from the disc, pairs of spicules which are the rudiments of the ambulacral ossicles (*amb. os.*), alternate with the first pairs of tube-feet. Even after they have attained considerable relative size these ossicles are in contact with each other only at their ends. Their lateral faces do not come into contact, nor are the half-pores formed thereon until some time later. Five plates now appear, one in the mid aboral line of each ray, and together forming a circlet which lies just outside the interradials. These are the first radials (Fig. 78, *rad.* I). In the same line radial succeeds radial until a continuous series is formed between the primary one and the terminal plate in each ray. The adult skeleton is completed by the development of adambulacral, marginal and inter-brachial plates. Spines appear as minute, tri-radiate spicules with a small up-standing ray along with the terminal plates, but pedicellariae do not appear on the latter until there are three radials in each ray.

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DESCRIPTION OF THE PLATES.

List of Reference Numerals and Letters.

I, II, III, IV, V = The rays according to Gemmill and MacBride.
1/2, 2/3, 3/4, 4/5, 5/1 = The interradii.
I′, II′, III′, IV′, V′ = The lobes of the hydrocoele.

ab. cir. v. = Aboral circular vessel.
abd. f. = Abductor fibres.
ab. per. sin. = Aboral perihaemal sinus.
ad. a. os. = Adambulacral ossicle.
a. d. p. = Anterior dorsal process.
ad. c. b. = Adoral ciliated band.
amb. os. = Ambulacral ossicle.
amb. pr. = Ambulacral pore.
amp. st. ca. = Ampulla of stone canal.
amp. t. ft. = Ampulla of tube-foot.
an. = Anus.
ant. coe. = Anterior coelom.
ap. l. m. = Apical longitudinal muscle.
ap. n. = Apical nerve.
arc. = Archenteron.
att. st. ca. = Attachment of stone canal.
ax. mus. = Axial muscle.
ax. or. = Axial organ.
ax. sin. = Axial sinus.
az. t. = Azygos or terminal tentacle.
bl. = Blastopore.
cil. = Cilia.
cir. or. hae. t. = Circum-oral haemal tissue.
cir. w. v. = Circum-oral water vessel.
co. sp. = Collecting space.
cr. (*mi.*) *ped.* = Crossed (minor) pedicellariæ.
cr. or. n. r. = Circum-oral nerve ring.
c. t. l. = Connective tissue layer.
cut. = Cuticle.
cutis = Cutis.
dm. br. = Dermal branchia.
dor. cen. = Dorso-central plate.
dr. sa. = Dorsal sac.
ect. = Ectoderm.
ep. = Epithelium.
ep. per. cav. = Epithelium of the perivisceral cavity.
ex. per. ca. = Extension of perihaemal canal to tube-feet.
eye. = Eye.
fus. = Anterior fusion of right and left coeloms.
gen. ap. = Genital aperture.
gen. hae. st. = Genital haemal strand.
g. hae. t. = Gastric haemal tuft.
gen. sin. = Genital sinus.
gr. mad. = Grooves of madreporite.
gon. = Gonad.
hep. cae. = Hepatic caeca.
hor. sep. = Horizontal septum.
h. p. ax. or. = Head process of axial organ.
in. c. t. l. = Inner connective tissue layer.
inf. tr. m. = Inferior transverse muscle.
in. m. l. = Inner muscular layer.
in. m. os. = Infero-marginal ossicles.
int. mad. ca. = Intramadreporic cavity.
in. per. ca. = Inner perihaemal canal.
int. = Intestine.
int. rad. = Inter-radial plate.
int. sep. = Inter-radial septum.
l. a. coe. = Left anterior coelom.
la. nr. = Lange's nerve.
lat. tr. amb. mus. = Lateral transverse ambulacral muscle.
l. c. = Left coelom.
l. m. coe. = Left middle coelom.
l. p. coe. = Left posterior coelom.
mad. = Madreporite.
mar. can. = Marginal canal.
m. bra. = Median brachium.
m. d. p. = Median dorsal process.
mes. = Mesentery.
ml. c. = Mulberry cells.
m. p. = Madreporic pore.
mth. = Mouth.
*mth.** = Position of mouth.
mu. c. = Mucus cells.
mus. l. = Muscular layer.
n. l. = Nerve layer.
n. r. = Nerve ring.

oc. mus. = Occlusor muscles.
od. = Odontophore.
oes. = Oesophagus.
op. cu. = Optic cushion.
opt. cp. = Optic cup.
os. = Ossicle.
ot. c. t. l. = Outer connective tissue layer.
ot. m. l. = Outer muscular layer.
out. per. ca. = Outer perihaemal canal.
pb. sin. = Peribranchial sinus.
p. can. = Pore canals.
p. d. p. = Postero-dorsal process.
ped. = Pedicellaria.
per. hae. ca. = Perihaemal canal.
per. = Peristome.
per. cav. = Perivisceral cavity.
p. l. p. = Postero-lateral process.
p. o. p. = Pre-oral process.
pr. o. c. b. = Pre-oral ciliated band.
pr. o. l. = Pre-oral lobe.
pt. o. c. b. = Post-oral ciliated band.
pt. or. p. = Post-oral process.
r. a. coe. = Right anterior coelom.
r. c. = Right coelom.
rad'. = Radial plate.
rad. hae. st. = Radial haemal strand.
rad. nr. = Radial nerve.
rad. per. ca. = Radial perihaemal canal.
rad. w. v. = Radial water vessel.
rec. = Rectum.
re. sa. = Rectal sac.
r. l. bra. = Right lateral brachium.
r. m. coe. = Right middle coelom.
r. m. st. = Retractor muscles of stomach.
r. p. coe. = Right posterior coelom.
sep. = Septum of radial canals.
*sep.** = Transverse septum.
sk. = Sucker of tube-foot.
sp. = Spine.
sp. m. os. = Supero-marginal ossicle.
st. ca. = Stone canal.
std. = Stomodoeum.
stk. = Stalk.
st. (ma) ped. = Straight (major) pedicellaria.
stom. = Stomach.
stom. (card.) = Cardiac portion of stomach.
stom. (pyl.) = Pyloric portion of stomach.
su = Sucker of brachiolaria.
sup. tr. m. = Superior transverse muscle.
tb. ft. = Tube-foot.
td. bd. = Tiedemann's bodies.
tml. = Terminal plate.

PLATE I.

Fig. 1. *Asterias rubens*, viewed from the aboral surface. Natural size.
Fig. 2. External surface of madreporite. × 10.
Fig. 3. Internal surface of madreporite. × 10.
Fig. 4. A spine from border of ambulacral groove, bearing a group of straight pedicellariae.
Fig. 5. Basal piece and blades of straight pedicellaria. × 60.
Fig. 6. A sessile straight pedicellaria. × 60.
Fig. 7. Longitudinal section of sessile straight pedicellaria. × 160.
Fig. 8. Longitudinal section of stalked straight pedicellaria. × 160.
Fig. 9. Transverse section of straight pedicellaria. × 160.
Fig. 10. Spine from aboral surface, surrounded by crossed pedicellariae. × 18.
Fig. 11. Group of crossed pedicellariae. × 60.
Fig. 12. A crossed pedicellaria. × 100.

PLATE II.

Fig. 13. *Asterias rubens*, viewed from the oral or actinal surface. Natural size.
Fig. 14. Vertical section of aboral body-wall. × 70.
Fig. 15. Longitudinal section of dermal branchia. × 150.
Fig. 16. Longitudinal and sagittal section of free end of tube-foot. × 145.
Fig. 17. Longitudinal and tangential section of sucker of tube-foot. × 130.
Fig. 18. Transverse section of sucker of tube-foot. × 200.
Fig. 19. "Mulberry" glands in ectoderm of aboral surface. × 700.
Fig. 20. Transverse section of oral end of axial organ. × 420.

Fig. 21. Longitudinal section of gonad of an *Asterias* 14 mm. in greater diameter. × 130.

Fig. 22. Dissection to show stone canal, axial organ and gastric haemal tufts *in situ.* × 3.

Fig. 23. Axial organ and gastric haemal tufts removed from axial sinus. × 3.

PLATE III.

Fig. 24. Diagram showing relative position of ossicles in transverse section of ray.

Fig. 25. Circum-oral ring of ossicles of *Asterias rubens.* × 3.

Fig. 26. Circum-oral ring of ossicles of Astropecten, sp. × 3.

Fig. 27. Ambulacral and lateral skeleton, after maceration in solution of potash. Natural size.

Fig. 28. Small piece of aboral body-wall mounted in balsam and viewed by transmitted light. × 18.

Fig. 29. Circum-oral and proximal ambulacral and adambulacral ossicles viewed from oral surface after maceration in solution of potash. Natural size.

Fig. 30. Ossicles of aboral surface of disc. Natural size.

PLATE IV.

Fig. 31. Dissection of *Asterias rubens* to show the alimentary canal and its appendages. Natural size.

Fig. 32. Vertical section of peristome. × 335.

Fig. 33. Vertical section of cardiac portion of stomach, near its oral end. × 485.

Fig. 34. Vertical section of cardiac portion of stomach. × 550.

Fig. 35. Vertical section of floor of pyloric portion of stomach. × 485.

Fig. 36. Vertical section of roof of pyloric portion of stomach. × 485.

Fig. 37. Longitudinal section of intestine. × 420.
Fig. 38. Transverse section of hepatic caecum. × 550.
Fig. 39. Transverse section of median ciliated fold of hepatic caecum. × 550.
Fig. 40. Transverse section of rectal sac. × 27.
Fig. 41. Part of transverse section of rectal sac. × 130.

PLATE V.

Fig. 43. Dissection of *Asterias rubens* to show the water-vascular system. Natural size.
Fig. 44. Vertical section of two adjacent ridges on the external surface of madreporite, showing the opening of a madreporic pore. × 225.
Fig. 45. Transverse sections of two madreporic pores, near their deeper ends. × 310.
Fig. 46. A tube-foot and its ampulla. × 10.
Fig. 47. Vertical section of ampulla of tube-foot. × 485.
Fig. 48. Part of longitudinal section of stone canal of specimen 11 mm. in greater diameter. × 340.
Fig. 49. Vertical section of Tiedemann's body. × 160.
Fig. 50. Part of section of Tiedemann's body, showing tubules cut transversely. × 550.

PLATE VI.

Fig. 51. Horizontal section of a large madreporite. × 20.
Fig. 52. Part of transverse section of axial organ. × 120.
Fig. 53. Part of longitudinal section of axial organ. × 120.
Fig. 54. Leucocytes from axial organ. × 700.
Fig. 55. Vertical section of madreporite and aboral end of stone canal of specimen 6 cm. in greater diameter, selected from a series passing through the madreporite from side to side. The middle of the disc of the animal lies on the left of the figure. × 75.

Fig. 56. Part of vertical section of disc of same specimen. × 125.

Fig. 57. Horizontal section of madreporic interradius of a disc about 5 mm. in diameter, showing the relative positions of the axial organ and the stone canal in the axial sinus. × 160.

PLATE VII.

Fig. 58. Longitudinal and sagittal section of tip of ray. × 45.

Fig. 59. Longitudinal and sagittal section of azygos or terminal tentacle. × 310.

Fig. 60. Transverse section of optic cushion. × 390.

Fig. 61. Longitudinal and sagittal section of optic cushion. × 310.

Fig. 62. Part of longitudinal section of free end of tube-foot. × 420.

Fig. 63. Vertical section of ectoderm near madreporite, showing cord-like thickening of nerve layer, *nl.** × 700.

Fig. 64. Various forms of pigmented cells from lining of optic cup. After Cuénot.

Fig. 65. Vertical section of optic cup. After Cuénot.

Fig. 66. Transverse section of radial nerve cord. × 200.

PLATE VIII.

Vertical section of *Asterias rubens* passing through the madreporic inter-radius and the proximal portion of the opposite ray. Diagrammatic.

PLATE IX.

Fig. 67. Dissection to show the gonads *in situ*. Natural size.

Fig. 68. Early bipinnaria a little older than that shown in text-figure VII. viewed from the ventral surface. × 130.

Fig. 69. Slightly older bipinnaria, viewed from the ventral surface. × 130.

Fig. 70. Bipinnaria about 21 days old, viewed from the dorsal surface. × 60. After Gemmill.

Fig. 71. Fully developed bipinnaria, viewed from the ventral surface. × 75.

Fig. 72. Early brachiolaria, about 38 days old. viewed from the ventral surface. Reduced, after Gemmill.

Fig. 73. Fully-developed brachiolaria, viewed from the left side. × 35. Partly after Gemmill. The developing skeletal plates are not shown.

Fig. 74. Brachiolaria undergoing metamorphosis. The darkly-shaded posterior portion represents the aboral surface of the disc of the young starfish. × 35. The developing skeletal plates are not shown in this nor in the previous figure.

Fig. 75. Young *Asterias forbesi* viewed from the aboral surface. × 50.

Fig. 76. Young *Asterias rubens*, attached by its sucker and stalk to a frond of seaweed, but ready to break away. After Gemmill.

Fig. 77. Young *Asterias forbesi*, slightly older than that represented in fig. 75. × 35. The skeletal plates are not shown.

Fig. 78. Young *Asterias rubens*, viewed from the aboral surface. × 35.

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Plate 1.

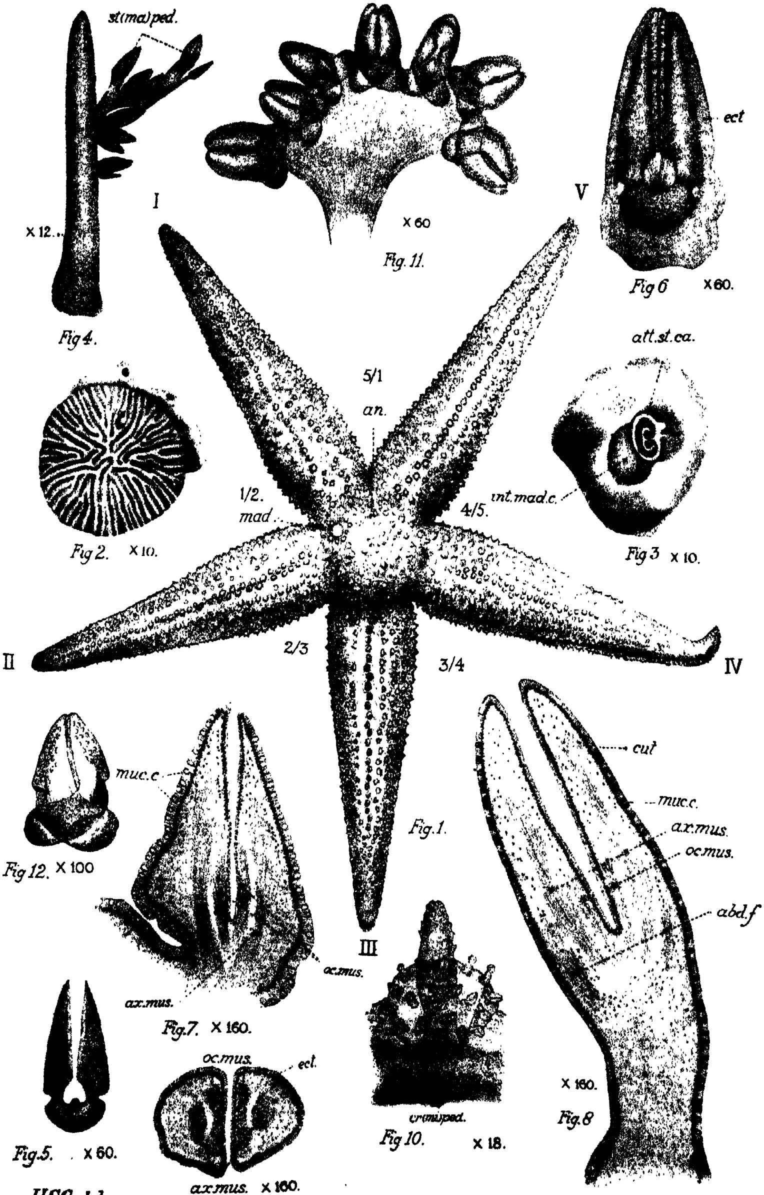

Fig 4. x 12.

Fig. 11. x 60

Fig 6 x 60.

Fig 2. x 10.

Fig 3 x 10.

Fig. 1.

Fig 12. x 100

Fig. 7. x 160.

Fig. 8 x 160.

Fig. 5. x 60.

Fig. 9. x 160.

Fig 10. x 18.

H.C.C. del.

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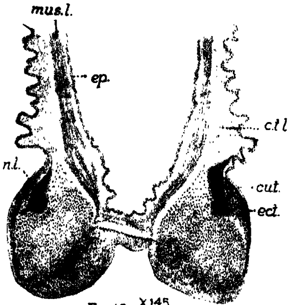
Plate II.



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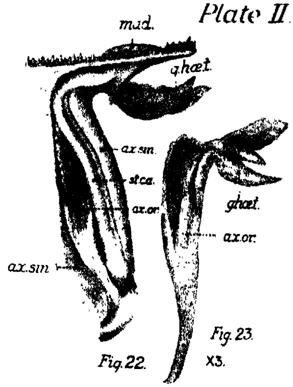
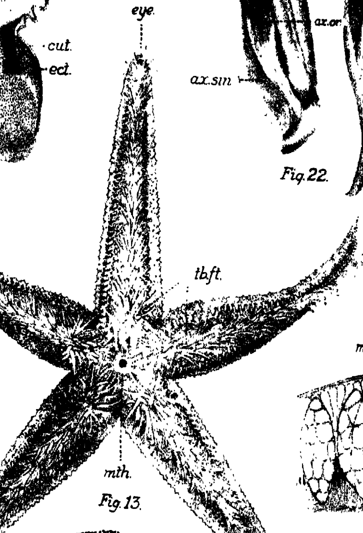


Fig. 22. Fig. 23. X3.



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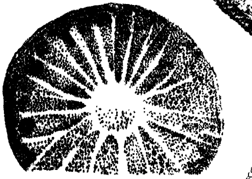

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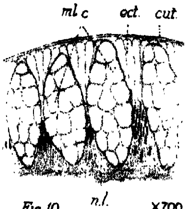
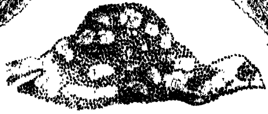


Fig. 19. X700.



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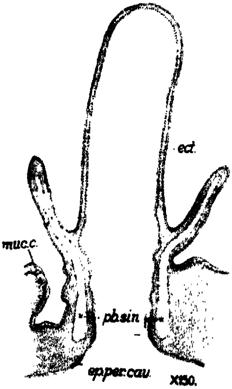

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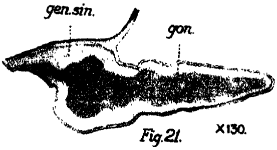

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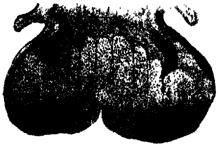

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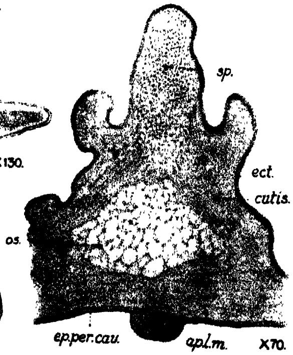

Fig. 14. X70.

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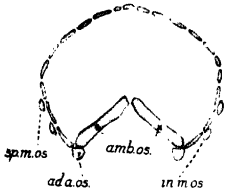
Plate III.



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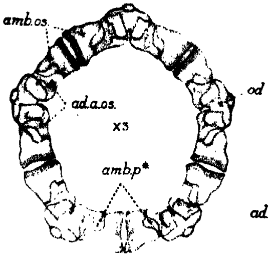

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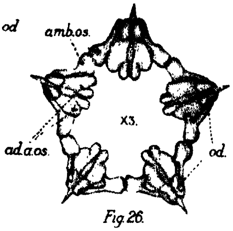

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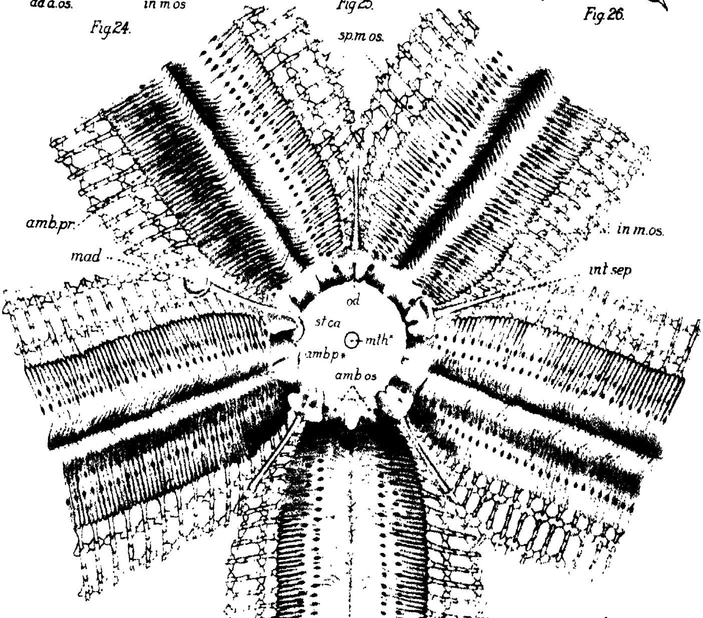

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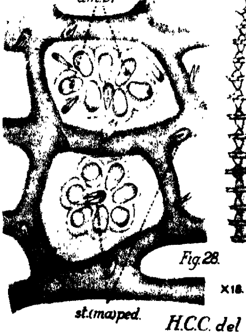

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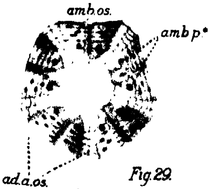

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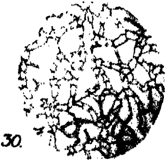

Fig.30.

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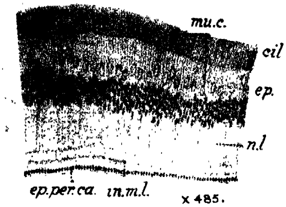
Plate IV.



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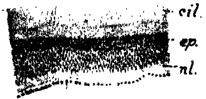

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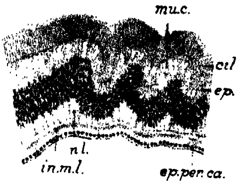

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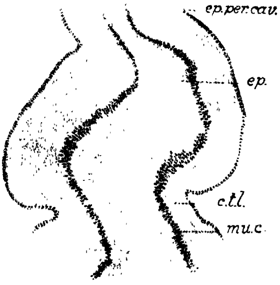

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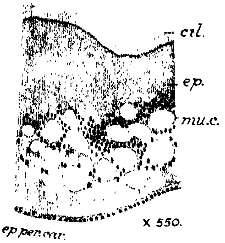

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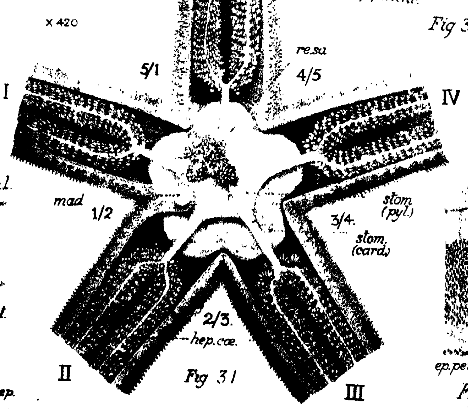

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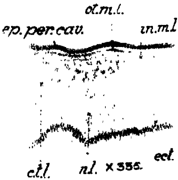

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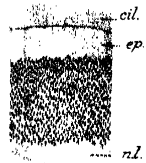

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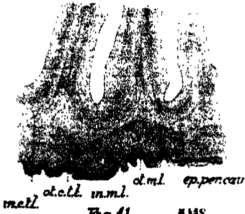

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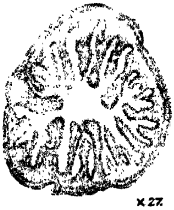

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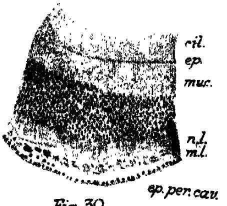

Fig 39. x 550.

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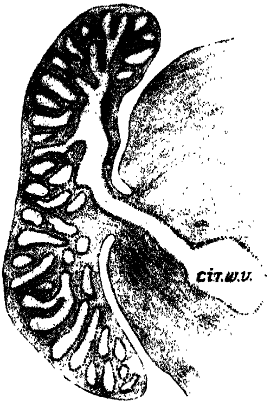
Plate V.



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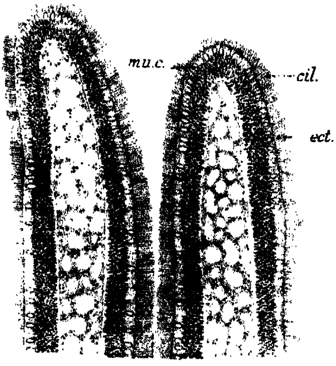

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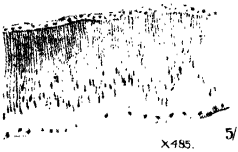

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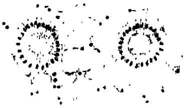

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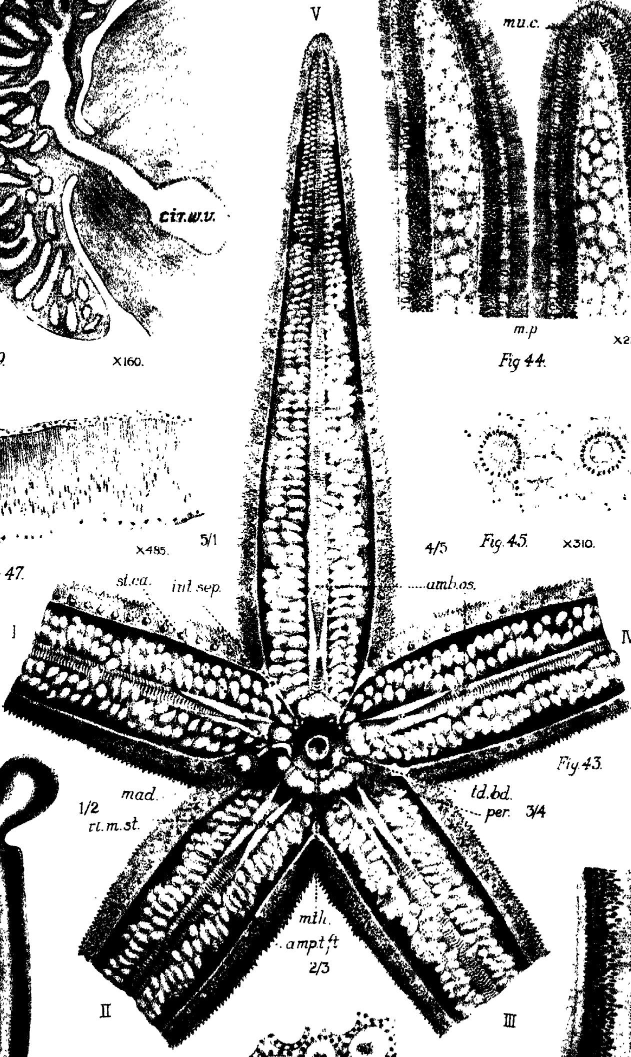

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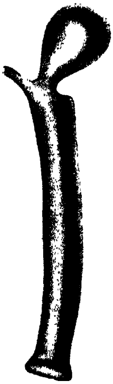

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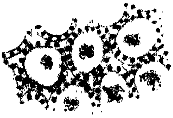

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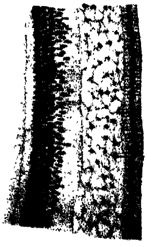

Fig. 48.

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Plate VI.

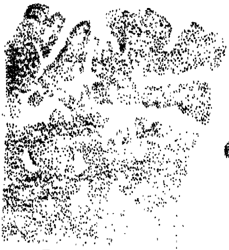
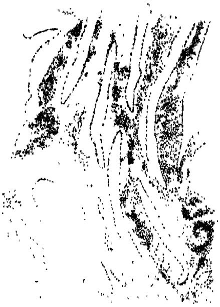


Fig. 52. x120.

Fig 54. x700



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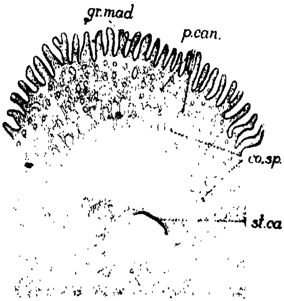

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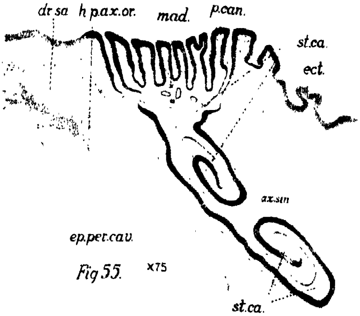
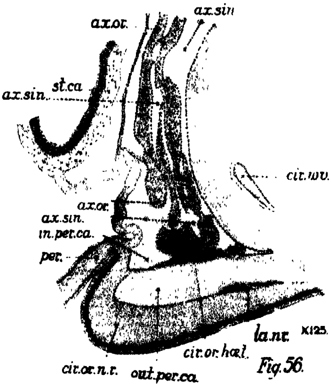


Fig 55. x75



x125. Fig. 56.

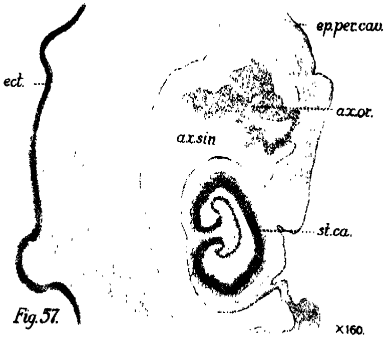


Fig. 57. x160.

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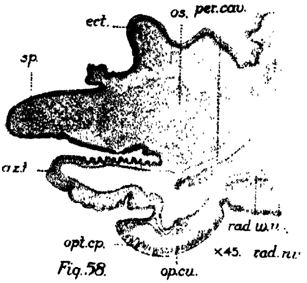

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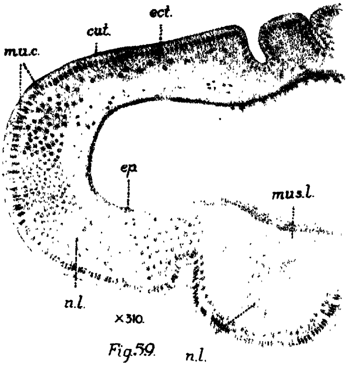

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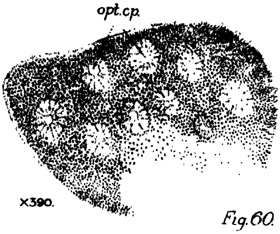

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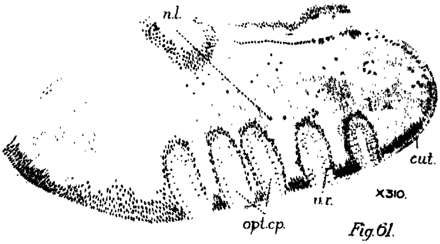

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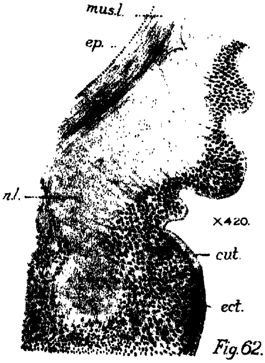

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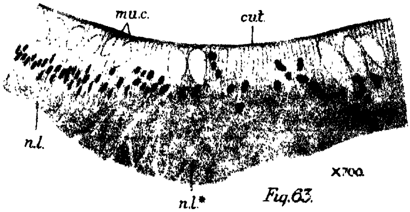
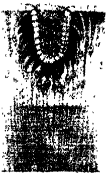


Fig. 63.

Fig. 64.



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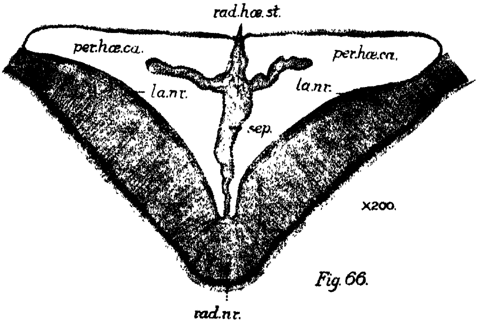

Fig. 66.

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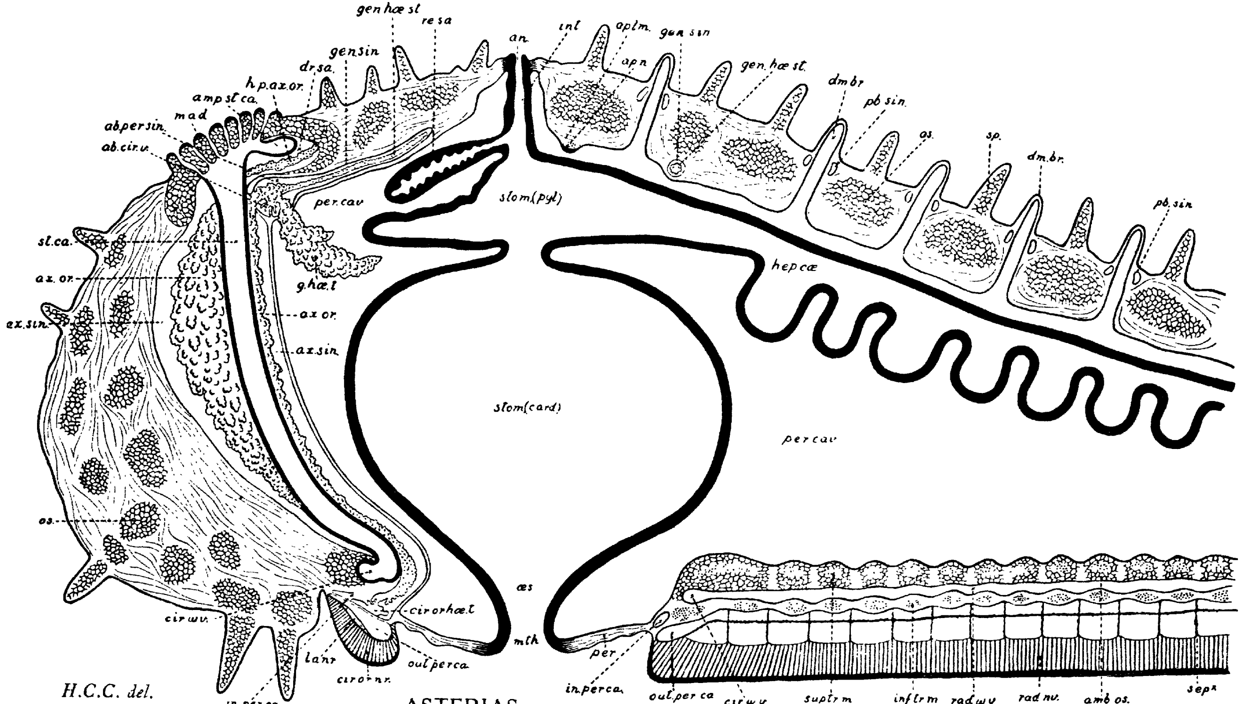

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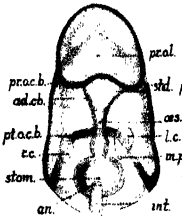
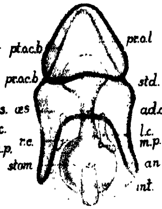


Fig.68. ×130



×130 Fig.69.

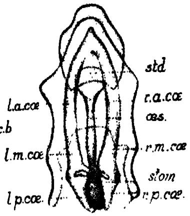


Fig.70.

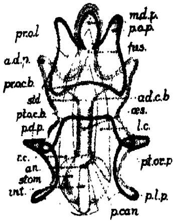


Fig.71. ×75

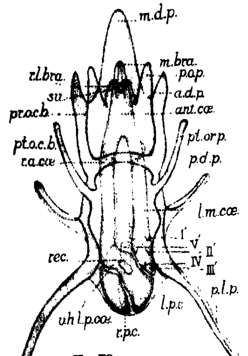


Fig.72.

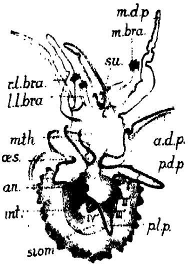


Fig.74. ×35.

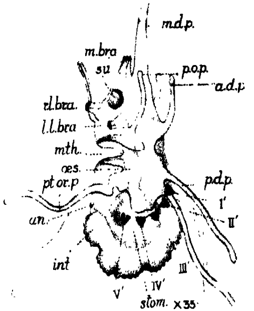


Fig.73. ×35

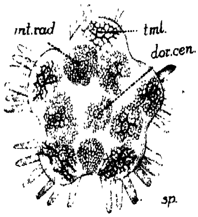


Fig.75. ×50.

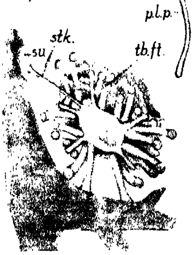

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Fig.76.

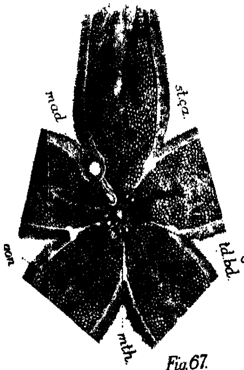


Fig.67.

H.C.C.del.

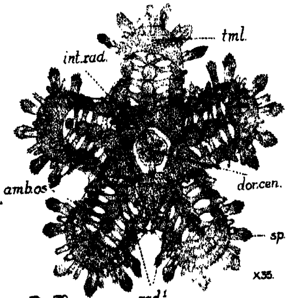
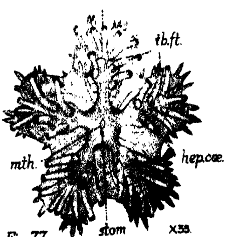


Fig.78. ×35.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tb.ft.
mth.
hep.cœ.
stom

Fig.77. ×35.

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